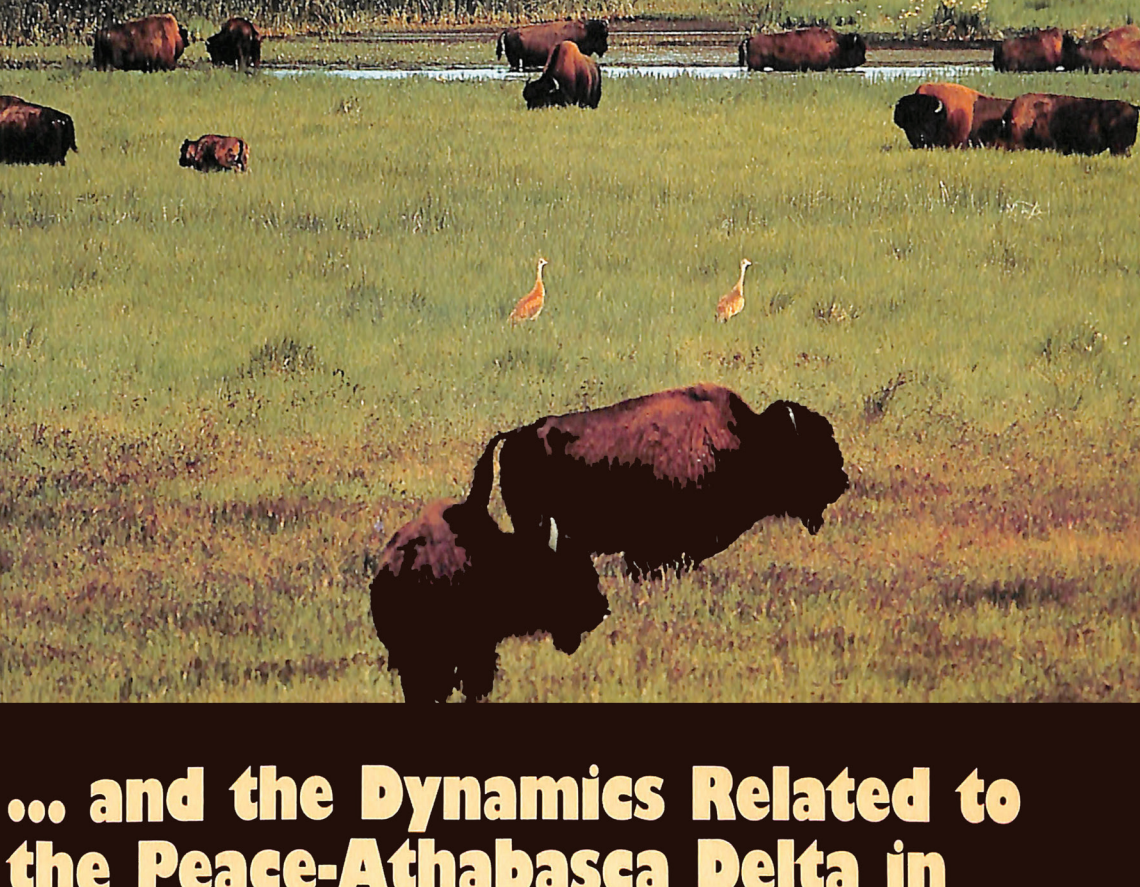
Wolves, Bison...



... and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park

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D.W. Anion

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S.M. Oosenbrug
D.W. Anions

with a foreword
by R.O. Peterson

Circumpolar Research Series Number 4
Canadian Circumpolar Institute
University of Alberta

This monograph is a timely review of a subject of public concern. Its sponsors take responsibility for focusing the topic and granting the authors freedom of inquiry. The book has also received extensive peer group review, however, all interpretations and findings provided here are those of the authors.

Ten percent of all the profits from the sale of this book will be donated to wolf conservation in India. In a time of rapid environmental degradation, it is the opinion of the authors that much more needs to be done in the developed world, while increased attention should also be directed towards solving problems in areas with the greatest human populations. This is in the spirit of the earth summit held in Rio de Janeiro in June 1992.

Canadian Cataloguing in Publication Data

Main entry under title:
Wolves, Bison and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park

(Canadian Circumpolar Research Series No. 4, ISSN 0068-0303)
Includes bibliographical references.
ISBN 0-919058-83-3
1. Bison, American — Wood Buffalo National Park. (Alta. and N.W.T.) 2. Wolves — Wood Buffalo National Park. (Alta. and N.W.T.) 3. Animal populations — Wood Buffalo National Park. (Alta. and N.W.T.) 4. Predation (Biology) I. Oosenbrug, S. II. Anions, D. III. Canadian Circumpolar Institute. IV. Title. V. Series: Research Series No. 4 (Canadian Circumpolar Institute).

QL737.C22C37 1993 599.73'58 C93-091312-4

1993 Carbyn, L.N.

Cover Design by Cathryn Shanks.
Printed by Art Design Printing Inc., Edmonton, Alberta, Canada

Frontispiece

Bison in the Peace-Athabasca Delta of
Wood Buffalo National Park

Dedication

We dedicate this book to the Northwest Mounted Police, Buffalo Rangers, Wardens and Patrolmen who, for about a century, spent much of their lives following the bison herds with dog teams, snow machines, vehicles and aircraft, to protect, count and study a truly unique animal population on the North American continent.

Foreword

It is a little over a century since humans nearly extirpated bison from the North American continent. Without the bison, the prairies and plains were quickly subdued. Carnivores, including native humans, long supported by the immense thundering herds of bison, were likewise eliminated.

This book deals with the modern aftershocks of that gigantic perturbation. It chronicles the discovery of wood bison in the far north, the resulting establishment of Wood Buffalo National Park, and the introduction of plains bison and associated diseases to the Park. Overlain are the ecological ramifications that followed construction of the Bennett Dam on the Peace River in the 1960s, upstream from the Park.

For decades Wood Buffalo National Park was the largest national park in existence. Its very name conjures up images of immense northern wilderness, beyond the heavy hand of technological humanity. Wood Buffalo today presents a harbinger of issues that may soon become commonplace in all large national parks. Priceless natural resources, beset by complex problems of human devising, will force increasingly serious challenges upon managers. Maintenance of the natural order, even determining what, exactly, that natural order is, will require ecological insights that exist today in only rudimentary form.

This study by Carbyn, Oosenbrug, and Anions is an important landmark in the long history of bison investigations in Wood Buffalo National Park. It comes at a critical juncture in the management history of the Park, as the future of the wood bison is again the subject of intense debate. The complexity of the modern management dilemma, and the importance of thorough ecological research, will be clear to all who follow the story.

Beyond its implied implications, this study is the only in-depth study of a predator-prey system that once dominated the mid section of the North American continent. The reader gains an appreciation of the mobility of huge herds of bison, linked to the shifting pulse of sedge meadow productivity. Here also are the largest wolves in the world in some of the largest packs documented. In this land of ecological superlatives, the ever adaptable wolf tops an ecological system that at once fascinates and challenges us.

Rolf O. Peterson
Professor of Wildlife Ecology
Michigan Technological University
Houghton, Michigan
15 July 1992

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SUMMARY

The number of bison (*Bison bison*) in the Wood Buffalo National Park region has changed dramatically since Europeans first recorded their presence in 1772. Numerical trends have been well documented, so that more historical information exists for these bison than for any other population of ungulates in Canada. We have divided the historical information into three eras - the early era (1772-1924), the management era (1925-1968), and the decline era (1969-1991). The status of bison from the early era was taken from scattered reports by explorers, naturalists, and government officials. At the beginning of the management era, plains bison (*B. b. bison*) were introduced into the area. This had dramatic consequences, and ramifications have plagued management of the herd ever since. The number of resident northern or wood bison (*B. b. athabascae*) had passed its lowest level (estimated between 500 to 1,500 animals) in the early 1920s. The introduction of plains bison triggered a series of events. The two subspecies interbred and as the mixed population increased, it extended its range into new areas. In Alberta the legal status of wood bison has led to some difficulties in interpretation. We have included a brief overview of the wood bison recovery program in Canada, because the seed stock for the program came from Wood Buffalo National Park.

A surprising revelation to us, after an examination of historical documents, was the general absence of information on bison in the Peace-Athabasca Delta prior to their introduction in the 1920s. Fort Chipewyan was considered a "fish fort", while posts along the upper and central Peace River area were "buffalo posts". Only after the 1925-1928 introductions did bison appear to become a major faunal element of the Peace-Athabasca Delta within historical times. That is, however, not to imply that bison were absent from the area.

Between 1971 and 1991, the number of bison in Wood Buffalo National Park declined rapidly. The population had been estimated at approximately 10,000 in 1971; by 1991 the number was estimated at approximately 3,400. Surveys conducted by wardens indicated that the decline began around 1970. Subsequently, the massive drowning of some 3,000 bison during the spring of 1974 appears to have been an important single factor that accelerated the already existing downward trend. Once the population was reduced to lower levels, habitat changes, predation, and disease appeared to continue to suppress numbers, as mortality rates exceeded recruitment. Bison declines in the Park accelerated after cessation of predator control programs that were in place from the mid 1930s to the mid 1960s. Cause and effect relationships on this issue cannot be reconstructed in retrospect, but inferences can be made.

The decline of bison has been more rapid in the area south of the Peace River. Over a 20-year period there has been an increase in the proportion of bison north of the river. In the 1971-1976 period, the population north of the river comprised about 15% of the total, while from 1986 to 1991 it represented about 38% of the total population. The interval trend changes were 12% (1974), 29% (1980), 33% (1987) and 38% (1991). The bison population declined over a 20-year period by a factor of about 3.2 while analysis of satellite imagery over 13 years (1976-1989) indicated a loss of productive habitat by a factor of about 2.

The decline in the bison population is reviewed in light of the severity of winters, changing conditions in the hydrological regime of the Peace-Athabasca Delta, wolf predation, and the effects of diseases. The information on bison distribution and population levels was collected during wardens' surveys conducted between 1971 and 1991. More than 23,000 data entries were collected between 1971 to 1981 by at least 48 investigators, in an excess of 3,000 flying hours for the total period. Data for the period from 1981 to 1991 were also reviewed in order to update information on trends up to 1991. Results from predator and prey studies are included for the periods of 1978 to 1981 and 1985 to 1991. Distribution and migration of bison were observed from aerial surveys. Anthrax surveillance flights over the years recorded 365 deaths from this disease.

The Peace-Athabasca Delta (south of the Peace River) is still the most important primary winter and summer range for bison in Wood Buffalo National Park. North of the Peace River, the primary winter ranges are associated with the Slave River lowlands and with adjacent meadows along three creeks. Recent aerial tracking of bison by Parks Canada staff of the Canadian Parks Service indicate that four subpopulations exist in the northern area. These occur in the Pine Lake, Little Buffalo River, Needle Lake, and in the Garden River areas.

During midwinter, approximately 80% of the bison in the Park are distributed over primary ranges. Optimum habitat for bison is largely composed of sedge meadows, which in the Delta are associated with the areas of fluctuating water levels. In the open Delta, optimum habitat occurs primarily between contour elevations of 209.25 and 209.85 m above sea level (asl). The vegetation in and around perched basins, which are affected by floods that exceed 209.85 m, is also important to bison, as well as to many other species of wildlife (e.g., waterfowl, muskrats). Construction of the Bennett Dam (upstream on the Peace River) has influenced delta ecology. Completion of the dam and subsequent annual filling of the dam has changed the spring run-off patterns. Water levels were lower than average between 1968 and 1971, above average between 1972 and 1974, and average to low between 1975 and 1978, followed by marked drought conditions between 1979 and 1981.

The process of habitat changes in the Delta continued to 1991. One study concluded that the productive vegetation communities have decreased throughout the entire Delta from 126,500 ha in 1976 to 97,900 ha in 1989. While this amounts to a reduction of productive wetlands of 23%, the loss actually represents a 47% reduction in that area of the Delta where wetland habitat is the dominant habitat

type. Further study shows that the most productive perched basin portions of the Delta were further reduced from 33% to 65% of the productive vegetation communities from 1976 to 1989. Modelling using satellite imagery has indicated that unless hydrologic conditions change from the patterns existing since 1976, almost two-thirds of the potentially productive wetland habitat will be lost by the year 2035. Ground observation in the Delta confirm that portions are rapidly changing and that bison ranges are being lost, hence concentrating bison in smaller areas. Important range studies in the Delta were carried out in the mid 1970s. It is essential to continue such studies in the future.

The snow cover influences the foraging behavior of bison. Bison penetrate the snow using their massive heads by swinging from side-to- side, by pushing upwards with nose and forehead, and by an inward chin pull. Winter severity was assessed using several criteria. The criteria were snow density, snow depth, the duration of the period of critical snow depth (DPCSD), and windchill values. Critical snow density values (.20) were rarely reached or exceeded in Wood Buffalo National Park. The mean annual snow depth was significantly greater at Fort Chipewyan than at Fort Smith. The duration of the period of critical snow depth was significantly longer at Fort Chipewyan than at Fort Smith, but snow cover persisted longer at Fort Smith. On the basis of windchill values, the winters of 1971/72 and 1973/74 were the coldest at Fort Smith and Fort Chipewyan respectively. The data suggests that, in terms of its impact on bison, the DPCSD is the most useful criterion for assessing winter severity. Winters were most severe during 1973/74 and 1975/76. On the average, winters were more severe during the period in which the number of bison sharply declined (1971-1974) than they were during the period in which the number was stable or slowly declining (1975-1981).

Although total counts made by wardens were useful in establishing population trends, the data were not consistent enough to demonstrate an annual cycle in herd-size dynamics. Analysis of the available data indicate that in all years, average herd size increased between the calving (1 April to 15 June) and post-calving (16 June to 31 July) periods. There is no evidence that the size of herds changed significantly between the post-calving and peak rutting periods (1 August to 30 September). Over the years, average herd size declined as the overall population declined.

From ground observations of bison at close range, it was noted that about 1% of the bison appeared to be severely debilitated. We assumed that this was the result of a combination of diseases and old age. About 1-2% of the bison had portions of their tails missing. Observations revealed that at least some of this was the result of attacks by wolves. Numerous cases of injuries to calves were observed and this was accompanied by evidence of blood poisoning. We believe that this condition is caused by a commensal bacteria (*Pasteurella multocida*) present in the mouths of carnivores.

The relationship between bison and wolves (*Canis lupus*) in Wood Buffalo National Park was investigated by radio-collaring wolves during the years 1978 to 1981, and by naturalistic studies from 1985 to 1991. Forty-three wolves were

collared and radio-tracking provided information on population estimates, home range sizes, pack sizes, territoriality, dispersal, movements, and predator/prey interactions. Of the 43 wolves, 23 were light coloured, 15 black, and five brown. Weights of wolves ranged from 40 to 59 kg for males (average 50 kg), and from 36 to 43 kg for females (average 40 kg). Observational work from 1985 to 1991 provided data on predation by wolves on bison calves during 116 days of close contact with wolves and bison in the Delta. Information on general wolf population trends was obtained from midwinter aerial surveys of bison from 1970 to 1991.

Wolf numbers were low in the 1950s and 1960s. Numbers increased rapidly in the early 1970s. From 1971 to 1974 numbers were at their highest. Average pack sizes were high, at the highest densities. Numbers were lower from 1977 to 1983 and increased again by 1990.

Mean pack sizes, obtained from routine surveys during 1979 to 1981, ranged from a high of 14.5 in 1973/74 to a low of 6.0 animals in 1975/76 and 1978/79. The percentage of single pairs ranged from a low of 6% in 1971/72 to a high of 53% in the post flooding period (1975/76). Large pack sizes preceded the major spring flood in 1974; flooding and increased trapping in the Peace-Athabasca Delta probably disrupted pack structure and reduced pack sizes in the mid 1970s. Human related mortalities of the wolf population declined significantly in the mid 1980s to early 1990s.

Territory sizes of wolves in Area I (north of the Peace River) of Wood Buffalo National Park were large. The composite territory of one pack over a three year period was close to 3,000 km^2, though the annual range used was around 1,000 km^2 in size. Average winter territory size was 728 km^2. Areas most frequently used by resident packs were considerably smaller than the overall area occupied. Pack members generally formed more cohesive units in winter, at a time when mating activity (mid February) and den construction (mid March) occurred. However, temporary splitting and reforming of packs during winter was common. Observations were made of non-pack wolves that appeared to be loosely associated with the territory of the Hornaday pack. In summer, pack members were more dispersed, often separated by as much as 35 km on any one day. The average same day distance between pack members during summer was 11.2 km, indicating that hunting in summer occurred with sub-units of packs ranging over large areas.

Wolves shifted centers of activities within their home range from winter to summer (mean distance 12.8 km), probably in response to seasonal shifts in food resources. Annual activities within territories indicated strong preference for some areas over others; wolves preferred open meadows, which comprised prime winter habitat for bison, over forested areas. Overlap in areas used by different packs was evident. In some instances wolves which trespassed into adjacent territories in Area I were killed by the resident pack. The same pack maintained a home range core exclusive of other packs, but ranged outside this core area in response to bison movements.

Ground observations in Area II (Delta) differed from results of aerial tracking in Area I. Wolf packs were heavily concentrated in restricted portions of the Delta

where bison concentrations were greatest at certain times of the year. No aggression was noted between three packs or subunits of 26, 18 and 12 individuals ranging over approximately 175 km^2 of Delta lands that contained large bison herds. Extreme concentrations of wolves were observed in October 1990, when the density was estimated at one wolf per 2.56 km^2 for a confined portion of the Delta. Wolf densities in Area I varied from a low of one wolf per 125 km^2 to a high of one wolf per 46 km^2. Comparable data for Area II was a low of one wolf per 104 km^2 to a high of one wolf per 38 km^2.

Winter conditions affected activity patterns of wolf packs. Travel distances by wolves decreased from early to late winter. In winters with less than average snow depth, wolves travelled less and killed more frequently than in more severe winters. Average distance between kills in Area I was 57.5 km. Predation by one pack was most common in the center of their territory. Comparable data was not obtained for Area II; however, limited ground observations indicated a concentration of kills at certain times of the year. Along migration trails monitoring of one pack indicated that in excess of 50% of time was spent in the proximity of herds.

We documented a total of 143 wolf/bison interactions. Sequences of encounters ranged from a recognition phase, to an approach phase, to a charge, and finally to a sustained chase. Of 65 wolf/prey encounters that were observed from aircraft, wolves were seen to closely watch the prey in 29 cases, and in 18 incidents, wolves approached, but did not attack. Attacks were recorded in 13 cases. On 55% of the wolf charges (12 out of 22 occasions), bison first stood their ground, but then fled. In all cases where bison fled, wolves attacked. Chase distances to full-pursuit by wolves did not exceed 500 m at a time, but total distances travelled by bison to escape wolves were often long. A maximum distance of 86 km was recorded for one herd.

Bison herd responses to attacking wolves were partly influenced by the number of previous attacks and the length of time they were exposed to wolves. Killing success increased with increased time that one pack spent associated with target herds. The longest time that this pack remained with a herd was six days. If the pack stayed with a herd for three or more days, it was successful in killing a bison. Killing success increased as time between kills increased. However, there was no apparent relationship between the pack's "active" interest in prey and elapsed time since its last kill.

Predation rates and prey selection in winter were studied in Area I from 1978 to 1981 on 285 contact days. During this period, one pack killed 40 bison and two moose, averaging one animal every 6.8 days. Generally, calves and old animals were the most vulnerable components of the bison population. Of all calf and yearling kills, 41% occurred in forest cover. Utilization was high in all years. Calves in winter were consumed within one day of being killed. Carcasses of adult bison were at times abandoned before being totally consumed, but in all cases, carcasses were completely utilized within one month. One pack studied spent an average of 2.4 days at each bison kill. Calculated food intake by this pack in midwinter varied from 6.4 kg per wolf per day to 2.5 kg per wolf per day. Average utilization per

wolf was 4.3 kg of food per day for an annual estimate of 5 bison per wolf (calves, yearling, adults).

Of 131 kills examined from winter predation, calves were killed at a disproportionately higher rate (24%) than their presence in the population (11%). Overall conclusions from examination of 2,928 wolf scat samples were that bison comprised 88% of total relative biomass consumed in winter and 70% in summer. We noted that methods used to determine diets of wolves had an important bearing on results. Direct observation of kills compared with results from analysis of scat samples provides different perspectives on food habits. Kill information does not include data about predation on smaller mammals.

Wolf and bison numbers remained stable throughout the duration of the 3-year radiotelemetry study (1978-1981). A combination of lower than maximum calf production and wolf predation is considered to be important in bison declines. The role of diseases in free-ranging bison is largely unknown and could be important in reproduction. Information on the overall impact of diseases on the dynamics of the Wood Buffalo National Park bison population is still lacking. Wolf predation had an impact on bison population dynamics, largely by reducing calf recruitment. The wolf-bison system north of the Peace River differs from that south of the Peace River, in terms of less bison concentrations, smaller herd size and greater interspersion of open areas with forest cover. These interrelationships require further study.

Areas north of the Peace River contain important ranges for bison (particularly in winter), but also have many small meadows, interspersed over larger areas with bogs and fens, jack pine ridges, boreal forest and aspen parkland, creating a mosaic of landscape features quite different from the extensive sedge meadows in the Delta. We hypothesize that this difference may result in greater bison dispersion, and less vulnerability of bison to wolf predation north of the river compared to areas south of the river. We do not rule out the possibility that future declines in Area I may be precipitated by predation, either by itself or in combination with other factors.

Classification of bison herds in spring/early summer (late May/early June from 1989 to 1991) indicated calf/cow ratios of 22, 30 and 31 ($\overline{X} = 28$) per 100 cows. Comparable fall counts resulted in ratios of 11, 17 and 21 ($\overline{X} = 16$) per 100 cows. Calf losses on average for the 3 years from spring to fall was 44%. Calf survival from spring counts to the next year was an average of five per 100 cows. Earlier studies (1978 to 1981), indicated an 8% recruitment rate of calves into the yearling category. This low recruitment rate was insufficient to offset losses of adults, calves and yearlings to wolf predation, disease and other sources of mortality within the system. Ground observations indicated that one pack of seven adult and subadult wolves killed a minimum of eight calves in 8 days. On another occasion a pack (believed to number 26 wolves) killed three calves in one attack in October. The behaviour of cows, after losing a calf, provided quantitative information on calf losses.

A comparison of bison population declines north of the river, with those south of the river, reveals some interesting differences. The significance of this finding is discussed in detail using several models. We have concluded from this study, that in the wolf/bison system of Wood Buffalo National Park, both autecological characteristics of the species (i.e., behavioral characteristics) and environmental conditions are ultimately important determinants of predation risks for bison. Physical changes in the landscape, e.g., drying of the Delta, or other new perturbations (fire, flooding) can rapidly change the balance between different habitat components. Therefore, the relationship of proximate factors (e.g., wolf predation possibly causing the observed decline in bison) may well be linked to ultimate factors (drying of the Delta, diseases in bison), which cannot be as readily measured. The real impact that wolf predation had on the bison population was studied in detail, and our conclusions are similar to those of J. Dewey Soper who worked in the Park in the 1930s and 1940s.

This study is wide ranging in scope. We do not believe that our conclusions can be applied to other situations under varying conditions. There may well be underlying principles that have yet to be discovered, as the complexity of the ecosystem is immense.

1 Introduction

The geographic area that once formed the bed of McConnell Glacial Lake provides suitable environments for the largest complex of free-roaming bison herds in North America (Figure 1). The nature of the surficial geology of portions of the McConnell Lake bed resulted in soil conditions suitable for growth of sedge meadows that constitute bison winter range. These herds comprise three population clusters north and south of Great Slave Lake (Figure 2), notably the Mackenzie Bison Sanctuary herds (estimated population of 2,040 bison in 1989 and the numbers declined to 1,600 by 1992), Wood Buffalo National Park herds (estimated population of 3,400 bison in 1990), and the Slave River lowlands herds (estimated population of 300-400 bison in 1990). A closer look at the Wood Buffalo population reveals that there are at least two herds, one north of the Peace River (Area I), and the other south of the Peace River (Area II) (Figure 3). Smaller herds of less certain status are along the west end (Garden River area) of the Park along the Peace River. Collectively these bison are an important cultural and economic asset of the region, Canada and the world. The largest of all three populations are the Wood Buffalo National Park herds.

Wood Buffalo National Park is an area that encompasses a spectrum of features ranging from boreal forest, to a karst topography, to riparian white spruce forests that contain some of the largest trees in northern climatic zones, to one of the largest and most spectacular fresh water deltas in the world. The Peace-Athabasca Delta dominates the landscape in Area II and has been vital to the human history of the village of Fort Chipewyan and the ecology of bison and wolves in the area. The Park was established in 1922, and is a huge wilderness area (44,800 km^2 in size) that straddles the border between the Northwest Territories and the province of Alberta (Figure 2). The greatest length of the Park (north/south) is nearly 290 km and its width varies from about 166 km in the north to 128 km in the south.

The Delta, as well as the Mackenzie Bison Sanctuary, and the Slave River Lowlands, are all part of an area that once formed part of the McConnell Glacial Lake bed that existed some 10,000 years ago. Postglacial isostatic uplifts created conditions suitable for extensive wetlands and upland meadows, open forest glades and dense coniferous forests. Productivity of specific wetland sites is high. This is particularly the case of the Peace-Athabasca Delta area where, since 1925-1928, the highest concentrations of bison within the region occur. This herd occupies summer and winter ranges that appear to be partly separate from those used by bison in Area

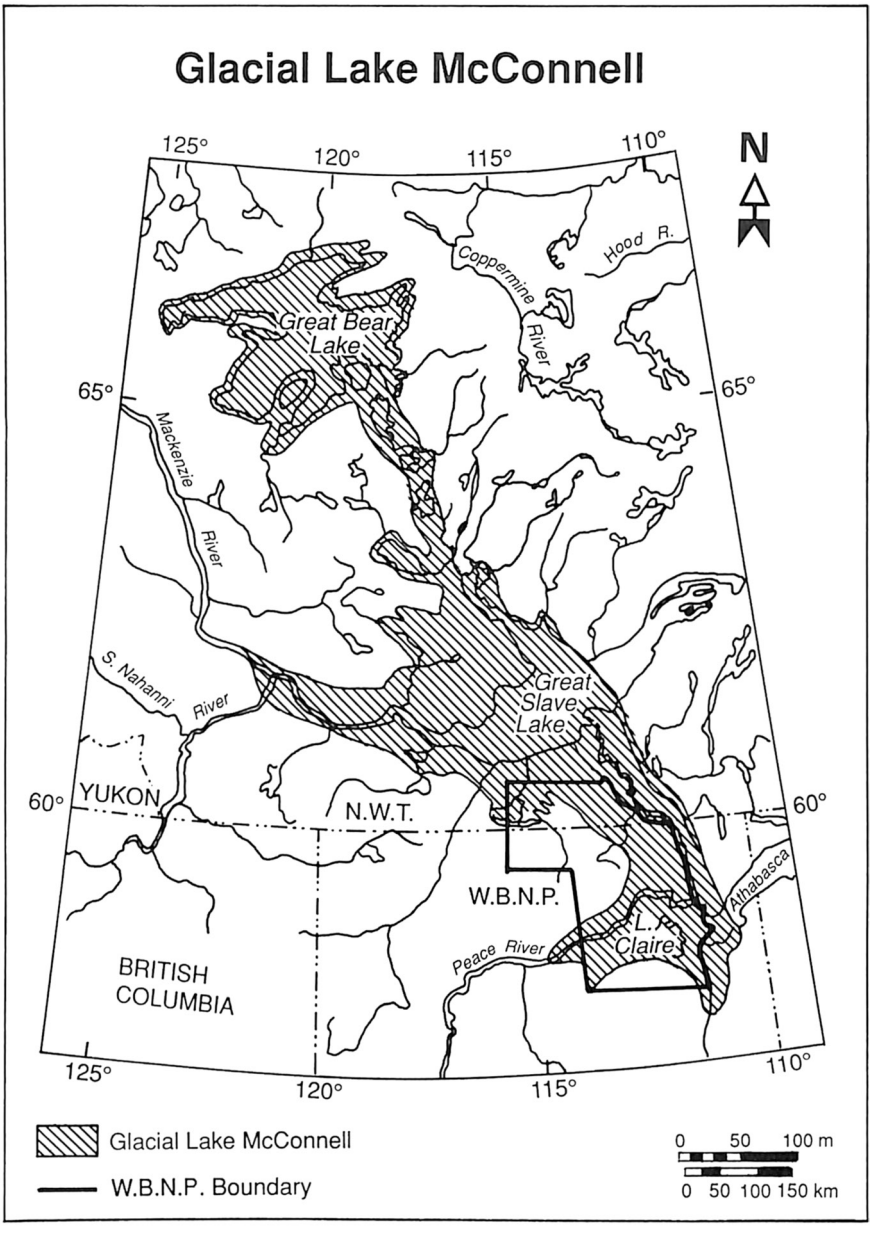

Figure 1. Outlined in cross hatching is the approximate extent of glacial Lake McConnell (Craig 1965) which, in the mid and southern edge, resulted in a surficial geology important to the growth of extensive sedge communities that provide suitable winter ranges for northern bison. In all cases, W.B.N.P. or WBNP refers to Wood Buffalo National Park.

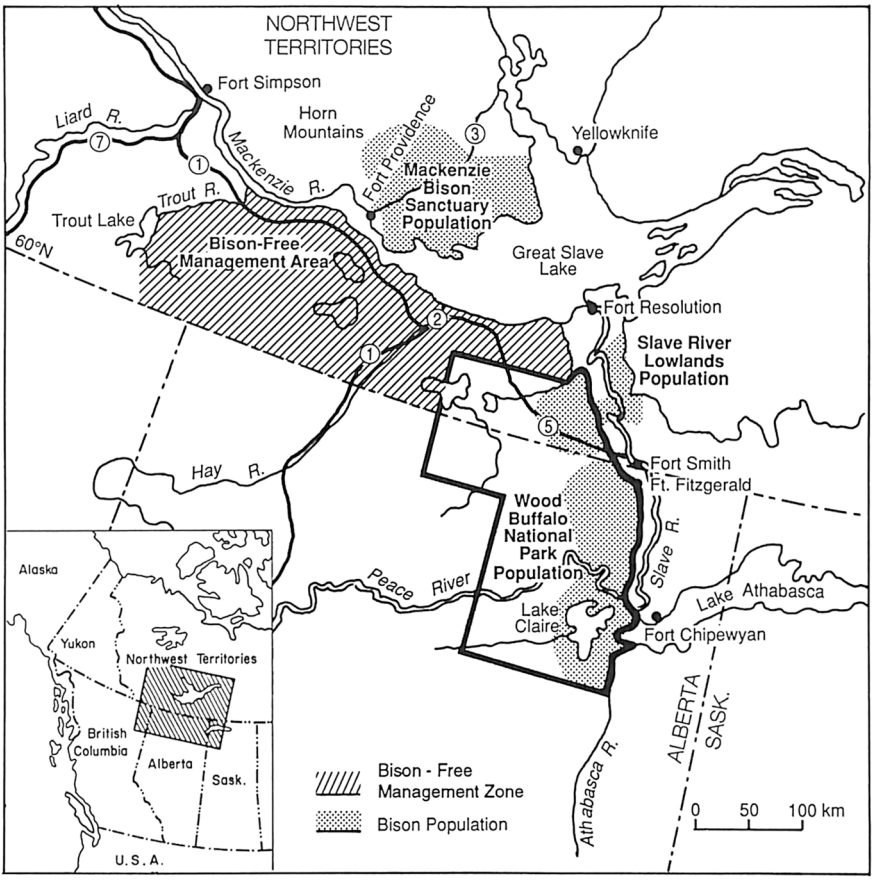

Figure 2. Distribution of three major bison populations around Great Slave Lake are shown. The northern herd in the Mackenzie Bison Sanctuary numbers over 2,000 (1989), while the Slave River population declined to about 300 animals. In the early 1990s the Wood Buffalo National Park population (both north and south of the Peace River) numbered around 3,500 animals. A bison-free zone was set up in 1987, in an attempt to reduce the risk of the spread of disease from Wood Buffalo National Park to the Mackenzie herd.

I, although interchange between ranges does occur. The relationships of the north/south distributions have evolved over a relatively short period of time, as discussed below.

Approximately 80% of the bison in Wood Buffalo National Park are associated with primary winter ranges, both north and south of the Peace River (Figure 3). Primary ranges cover approximately 9,000 km^2 (4,000 km^2 in Area I and 5,000 km^2 in Area II), leaving 35,800 km^2 within the Park as secondary ranges. Not only are the bison a spectacular wildlife feature of the landscape, but associated with these

herds are some of the highest densities of wolves found anywhere in North America. The principal prey for wolves in the primary ranges are bison (Oosenbrug and Carbyn 1982). Moose (*Alces alces*) are the only other important ungulates in the Park. Only a few moose are seen on the primary bison ranges south of the Peace River, and the species is more common in secondary bison ranges (Morgan 1989). Messier (1989) suggested that on primary bison ranges, bison are four times more numerous than moose (probably an overestimate of moose if both Areas I and II are considered) and moose are 14 times more numerous on secondary ranges. There

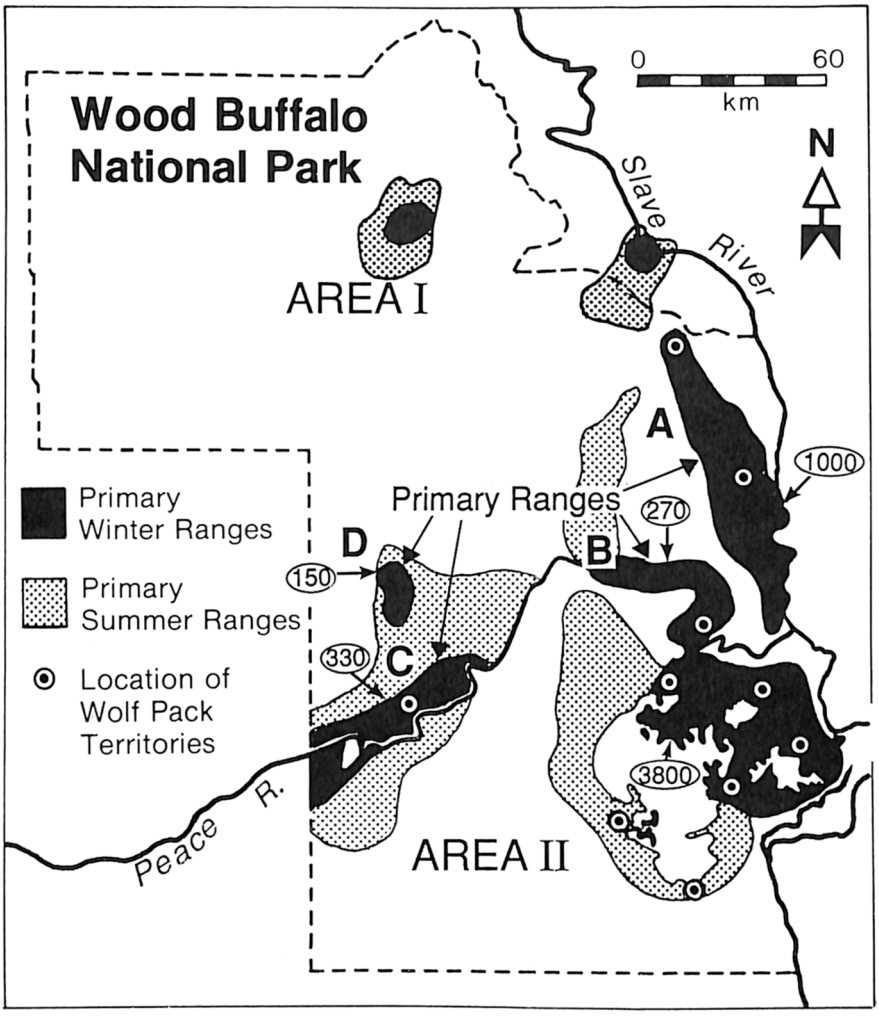

Figure 3. Overview of the primary winter ranges of bison in Wood Buffalo National Park. Numbers in circles indicate the mid to late winter counts for these areas as obtained from the 1981 surveys.

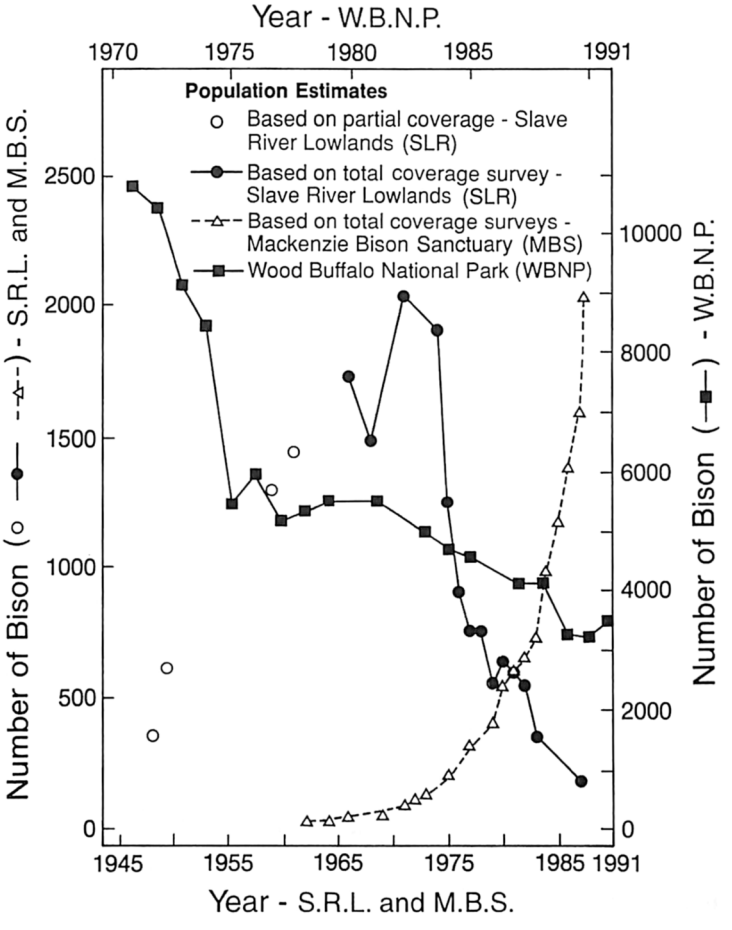

Figure 4. Population trends in bison in three populations within the Great Slave Lake, N.W.T. and Lake Athabasca, Alberta region. The populations are within Wood Buffalo National Park, Mackenzie Bison Sanctuary, and Slave River Lowlands.

is, therefore, within the Park, a "wolf-bison" system and a "wolf-moose" system. These systems overlap. Little is known about the wolf-moose system in the Park, whereas much more is known about the wolf-bison system. White-tailed deer (*Odocoileus virginianus*) occur only sporadically within the Park.

Numbers of bison plummeted from an estimated 10,000-11,000 in 1971 to 3,400 animals in 1990 (Figure 4; time scale in upper bar). This monograph deals with that decline and with the interrelationship of wolves and bison in North America's largest (second largest in the world) national park.

We drew upon three major sources of data. The first resulted from the vast amount of information gathered by the Park wardens. Data were collected on numeri-

cal status, distribution, and movements of bison. From 1971 to 1981 more than 2,000 hours were flown. The second source was from a 3-year intensive predator/prey study carried out from 1978 to 1981 when the movements, predation, and mortality of 43 radio-collared wolves were studied in detail. The third source was drawn from field work carried out from 1985 to 1991 in the Peace-Athabasca Delta (Area II).

Observational studies (1985-1991) focused on habituating wolves at rendezvous sites and following bison herds on their calving grounds, and during spring and fall migrations to obtain data on calf production. The habituation involved reducing flight responses by wolves to human observers by deliberately associating man with wolves at a time in their life cycle when the adults and subadults returned to rendezvous sites to feed the pups (Figure 5). Fear and avoidance responses of wild animals fade when the stimuli causing flight reactions are interpreted as "non-threatening" (Hediger 1980). Instances of extreme habituation of wolves have been recorded for arctic wolves at dump sites in which food was involved (Grace 1976). Such tameness was not desired in this study as the objective was to maintain continuous or near continuous observation of wolves and bison. To understand the process of habituation of wolves at rendezvous sites, it is necessary to gain an overview of the seasonal life cycle of a wolf pack (Murie 1944, Joslin 1967, Mech 1970).

The life cycle begins at nursery dens (Figure 5). Birth of pups occurs from late April to May. Emergence from nursery dens is followed by the establishment of activity areas known as rendezvous sites. It is at rendezvous sites that the process of habituation is best achieved. Foraging strategy of the adults is regulated by the fact that their movements radiate from these early summer activity sites. Adults bring the food to the young, either by carrying chunks of meat in their mouths or by regurgitating food from the stomach. Pups grow rapidly in the first 4 months of their lives and eventually join the adults in their hunting forays. By November, some preliminary participation in the attacks on bison by the pups is evident. Predation is most conspicuous in winter when packs kill their prey on their travel circuits in pursuit of their quarry. However, the impact on numbers is not necessarily greatest at that time of year. Predation pressures on calves often account for the removal of more individuals for a lower energy return.

The life history of all wolf packs in Wood Buffalo National Park, both north and south of the Peace River, as for other areas in the boreal forests, are similar. Differences between wolf/bison systems north and south of the river, however, likely pertain to geographic features and distribution of prey in the following ways:

1. Areas south of the river (Area II) contain large expanses of sedge meadows that are more or less contiguous.

2. Areas north of the river (Area I) contain smaller meadows spread over a larger area interspersed with bogs and fens, jack pine ridges, boreal forest and aspen parkland, creating a greater mosaic of landscape features than is the case for Area II.

3. The presence of alternate prey, particularly moose, is different, with fewer in the core delta areas (Area II) than in the areas north of the river (Area I).

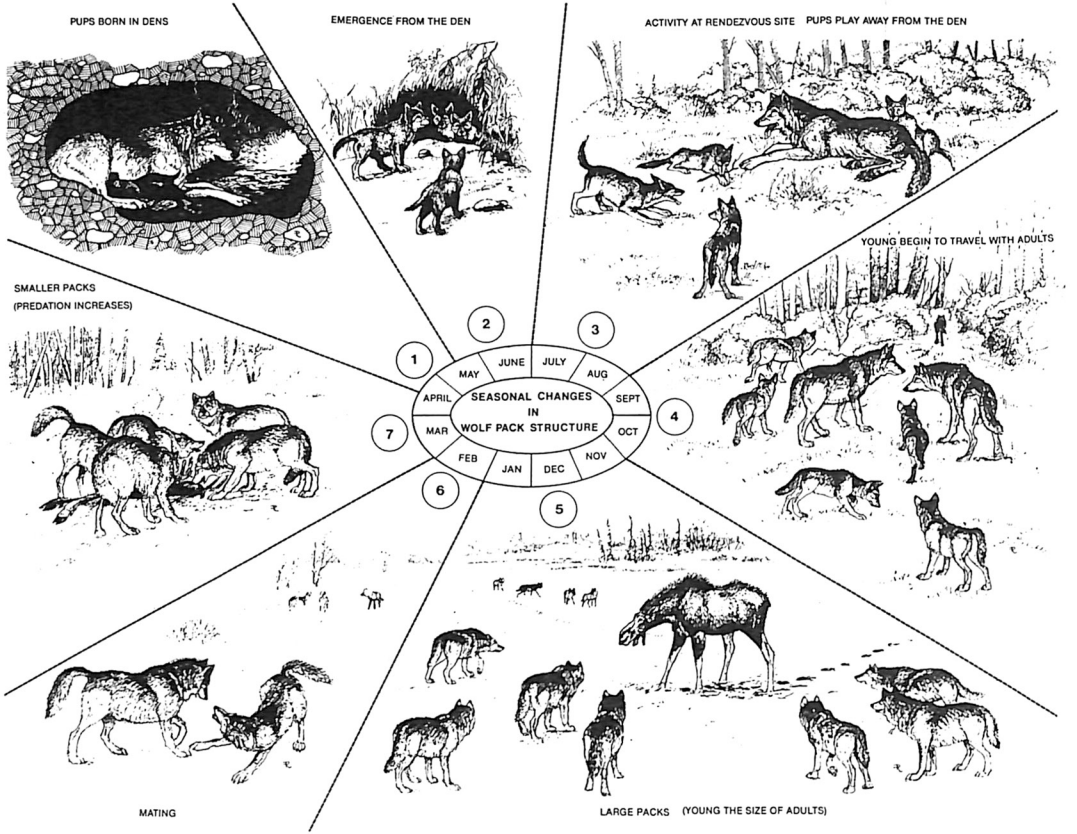

Figure 5. Illustration of the annual cycle of the life history of wolf pack dynamics in Wood Buffalo National Park.

Physiographic differences between Areas I and II appear to be important in the distribution of wolves and bison. We suspect that this may be related to the different search patterns by wolves and the resulting potential for more antipredator strategies by bison in areas with diverse habitat interspersions. If in fact bison vulnerability to wolf predation varies in different areas, and if predation is an important factor in the bison decline, then the impact of wolf predation would differ depending on habitat. Fraser (1985) pointed out the importance of treating subpopulations of a geographic area separately. Most populations are likely to contain several subpopulations, each with different rates of mortality, natality and recruitment, dictated by local variations in food availability and other environmental factors.

Bison declines south of the Peace River were analyzed separately from those north of the river. We have concluded that not only are autecological characteristics important (i.e., the behavioral adaptations of the predator and the prey populations), but of greater relevance may well be the total system in which the large carnivores act out their roles as predators. Therefore, habitat distribution and predator densities are important in the overall impact that predation has on the prey population.

The Wood Buffalo National Park herds consist of a composite of a remnant population of wood bison (identified as a subspecies) (*Bison bison athabascae*), and the introduced plains bison (*Bison bison bison*). The presence of these large herds in the area has attracted a great deal of attention, and more is known about their changing status over time than about any other large ungulate in Canada.

Historically these animals have frequently been the center of controversy. Management has ranged from test and slaughter for disease control, to small-scale slaughter to acquire meat for local use, to massive slaughters and export of the meat, together with large-scale vaccination roundups (Mitchell 1976), and suggestions of total annihilation using the sophisticated weaponry of the Royal Canadian Air Force (W. Stevens, pers. comm.). As a new century approaches, this population has once again become the center of attention. At issue is a disease eradication proposal because the diseases are of economic significance and the federal Department of Agriculture has a policy of disease eradication in domestic cattle that involves removing all infected stock.

In 1989, the federal Minister of the Environment appointed a five-member panel (Federal Environmental Assessment Review Office or FEARO) to conduct a public review of the status of diseases in bison in Wood Buffalo National Park. Once again the future of the bison population was the subject of debate and made national and international news headlines. In August 1990, the panel concluded that:

> "...eradication of the existing bison population is the only method of eliminating the risk of transmission of bovine brucellosis and tuberculosis from bison in and around Wood Buffalo National Park to domestic cattle, wood bison and humans. After considering the alternatives, the panel recommends that all free-ranging bison now living in Wood Buffalo National Park and surrounding areas be removed and replaced by disease-free wood bison".

Superimposed on the agricultural questions are those relating to rehabilitation of wood bison in northern areas. Threat of diseases for the Mackenzie Sanctuary bison herds and to game ranching further complicates the issue. A bison free zone was established by the Northwest Territories Department of Renewable Resources (see Figure 2) in 1987 to reduce the risk of spread of the diseases from Wood Buffalo National Park to the Mackenzie Bison Sanctuary. Three methods were employed (C. Gates, pers. comm.). These were: 1) aerial reconnaissance and ground pursuit of any bison seen in the zone, once spotted these bison were to be destroyed; 2) public participation by reporting sightings along highways, and 3) personal interviews with individuals working in the area. From 1987 to 1991 no bison were spotted during late winter aerial reconnaissance, however, several observations of bison and bison sign were reported during snow-free periods. From January to June 1992, at least 44 bison were detected in the bison free zone, nine of which were killed by departmental staff.

Biological implications of why some populations (Slave River Lowlands and Wood Buffalo National Park herds) have declined (Figure 4), while the Mackenzie Bison Sanctuary herd has until recently increased, are significant and set off a host of questions, not the least of which is "Why *did* the Wood Buffalo National Park herds decline while the Mackenzie population increased?" More specifically:

1. What has been the cause of the decline of bison in Wood Buffalo National Park?
2. Is there a threat of genetic contamination of free-roaming wood bison established in the Mackenzie Bison Sanctuary by the prairie/wood bison complex of Wood Buffalo National Park?
3. What are the implications of the existence of diseased bison to the potential restoration of wood bison in the boreal forest?
4. What is the threat of disease transmission from the bison to livestock?

The FEARO report suggests that if diseases are eliminated in Wood Buffalo National Park the population will be restored to higher levels. In reading the report, the implication is that disease is *the* most important factor in causing the bison decline. Quote: "No one factor can be identified as the cause of the decline. Tuberculosis and brucellosis *likely play a key role.*" This was an acceptance of Agriculture Canada's submissions to the Northern Diseased Bison Environmental Assessment Panel Hearings. One of Agriculture Canada's sources stated: "A comprehensive University of Saskatchewan study says they — i.e., those who claim disease is not a principal cause of the decline — are wrong. It found that mass drownings, water diversion schemes and severe winters cannot be blamed for the decline of the herds. The study also indicates that as a result of the diseases the Park herd will have died out in less than 10 years". Agriculture Canada's review of the factors that may have caused the decline did not include a thorough assessment of predation. The FEARO report did acknowledge that "...more recently predation by wolves, particularly on calves, may be chiefly responsible for low calf survival". The report further states that "...added to all of these

factors are the unknown effects of the change in hydrology and vegetation of the Peace-Athabasca Delta brought about by the W.A.C. Bennett Dam on the Peace River in British Columbia."

This monograph is an attempt to review the status of bison and to examine factors that may be contributing to the decline of the herds in the Park. In the first part we focus on the data collected by Park wardens during the years of decline (1971 to 1981). The results are discussed in relation to factors that may influence bison numbers, e.g., hydrological regime, winter severity, disease, predation, and poaching. For some parameters (e.g., fire history) data collected between 1981 and 1983 are included. An update of the most recent data on population trends, calf counts, and yearling survival collected during Park surveys conducted between 1982 and 1991 is also included.

The second portion of this monograph deals with the results of wolf studies in the Park, in which animals were radio-collared (1978-1981), and from observational work from 1985-1991. The predator-prey studies were more intensive and of shorter duration than the on-going, long-term monitoring programs carried out by the Warden Service. Data on calf survival and recruitment after 1985 were obtained by the Warden Service and by L. Carbyn from classified aerial/ground surveys.

In the absence of experimentation (a practice not acceptable within the confines of National Parks Policy), the only available options for research are observational work and examination of historical information. A more rigorous method to determine the factors responsible for the decline should be ideally framed by several hypotheses, listing the assumptions and deriving predictions. Three major hypotheses are outlined:

HYPOTHESIS A: The decline in bison numbers is primarily due to the diseases tuberculosis and brucellosis (position of proponents for Agriculture Canada).

Assumptions:

(a) The diseases were imported with prairie bison, during the transfers of 1925-1928.
(b) The diseases would have the same impact on the population dynamics of bison throughout the period of exposure.
(c) The diseases contribute 6% or less to the adult mortality (Fuller 1966, Tessaro 1987).
(d) Diseases affect calf production, fitness and survival.

Prediction:

(i) In an absence or reduction of incidence of the diseases the population would increase.
(ii) Diseases cause population decline by either preventing births or causing calf mortality and adult mortality in such a way that, when combined with other factors, results in annual mortality being higher than recruitment.
(iii) If diseases are causing the decline, then the effect would be the same north of the Peace River as it is south of the Peace River.

HYPOTHESIS B: *The observed decline from 1971 to 1991 was caused either by wolf predation, black bear predation or by a combination of the two.* (Called the predator hypothesis — see Section VII(3)(c).

Assumptions:
(a) Wolves are preying on bison throughout the range.
(b) Black bear (*Ursus americanus*) are preying on bison.
(c) Wolves are using bison as a major source of food.
(d) Black bear are using bison as a major source of food.

Prediction:
(i) In the absence of wolves, or if wolf numbers declined, bison numbers would increase.
(ii) In the absence of black bear, or if black bear numbers declined, bison numbers would increase.
(iii) When wolf/black bear numbers increase bison numbers will decrease.

HYPOTHESIS C: *The observed decline was not caused by any single factor, but was the result of a combination of factors.*

Assumptions:
(a) The combination of factors that caused the decline was present throughout the 1971-1991 period because, if the combination is important, removal of one or more of the factors would also change the impact.
(b) The complex of factors could not differentially allow a population to increase at one point in time and not another time, although it could find new combinations, i.e., it could be disease and predation at one time and poaching and flooding at another time.

Prediction:
(i) Bison would only decline in areas where the complex exists.
(ii) If any single factor is removed then the other factors remaining in place could not be important enough to cause the continued decline, because the hypothesis rests on the "complex" and not the single factor cause.

At the outset, we realized that some conclusions from observational work may not be justified if sample sizes were too small, or if conclusions could not be verified without experimentation. For example, survey results alone cannot be used to explain any observed changes in the bison population — detailed investigation of the functional relationships between population levels and environmental factors is necessary to complete the process. We believe that our work has set the stage for more detailed studies, some of which are currently in progress, but many of which are still required. Assembling the data to review the various factors that could have contributed to the observed bison population decline from 1971 to 1991 was a tedious process. We suggest, therefore, that the reader first review the discussion section before examining the data upon which the conclusions have been based.

II Historical Review

1. *Introduction*

Historical records on population trends span a period of over 200 years (Figure 6). An historical review is important in order to relate current population levels to those known from, or surmised about the past. Changes in the bison population are reviewed for each of three eras; the early or pristine era (1772-1924), the management (mid or manipulation) era (1925-1968), and the decline era (1969-1991). Impressions of the relative abundance of bison in the Great Slave Lake region during the late 18th and 19th centuries were derived from casual references in the reports of explorers and fur traders in the area. Information on relative abundance during the early to mid 20th century was derived from ground counts. In the last 40 years, aerial counts have been used increasingly as a means of estimating numbers.

The first reports of bison in the area were made by Hearne in 1772. For the purposes of our review, the early era extended from this point to the introduction of plains bison in 1925.

The first legal protection was set up for bison in 1877 in what has been called the Northwest Territories Game Ordinance Act. Protection was granted to animals aged 2 years or less. About 120 years after Hearne's visit, a geologist, William Ogilvie, was one of the first employees of the federal government to make recommendations on the protection of all bison in the area. In his report he recommended protective legislation (Ogilvie 1893). As a result the federal government in 1894 passed the *Unorganized Territories Game Preservation Act*. This Act was the first legislated intervention into the lives of native people in the region and prohibited hunting of wood bison, occupying ranges west of the Slave River. Though in place legally, the legislation was not enforced until 1897 (McCormack 1992). In 1899, *Treaty 8* was signed with some of the native people in the region, to extinguish native rights, by meeting with local Indian leaders and promising reserves and the right "...to pursue their usual vocation of hunting, trapping and fishing throughout the tract surrendered...subject to such regulation as may from time to time being made by the Government of the country." Establishment of special protective areas for bison became important in the next 25 years. A portion of the region was set aside as Wood Buffalo National Park during 1922 to "protect

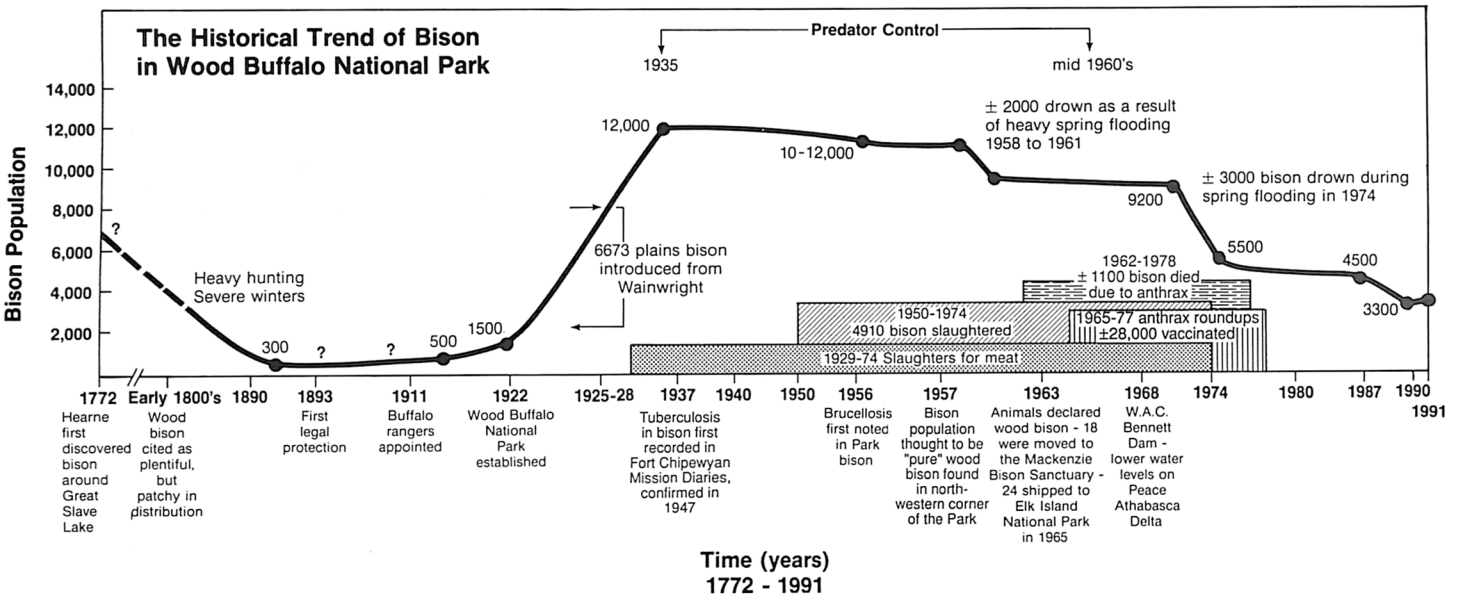

Figure 6. Summary of bison population trends from 1772 to 1991 in Wood Buffalo National Park.

wood bison in a 26,800 km^2 area north of the Peace River". In a sense, this could be considered the beginning of the management era; however, we chose to set the date at 1925, a year which marked the beginning of the introduction of 6,673 plains bison into the Park. These introductions had a major impact on the system; by 1926, the range of some of the introduced bison had extended south of the Peace River and into the Peace-Athabasca Delta. In that year, an additional 17,408 km^2 were added to the Park. With the introduction of plains bison came a 40 year period of slaughtering of bison for human consumption, predator control and attempts to control bovine diseases. This era ended with the completion of the Bennett Dam (1968), whereupon the decline era — one of protection and surveillance — began, and has continued until the present.

R. McFetridge (pers. comm.) provided the following review of the legal status of bison in the province of Alberta. He noted that there are some discrepancies in the records which need clarification.

The Northwest Game Act of 1906 appears to be the first wildlife legislation for the then newly established province. However, another Act, the Game Ordinance, passed in 1877, predates it. Records indicate that bison were big game and that licensed hunting was permitted, after 1 January 1912. North of the 55th degree of latitude unlicensed hunting for personal or family use may have been permitted at times, but the record is not clear. Hewitt (1921) says that under federal legislation, the Dominion Parliament provided a permanent closed season for buffalo for a number of years. There must have been some flexibility in the interpretation of the legislation.

In 1930, with the Natural Resources Transfer Agreement, bison were protected as un-hunted big game species under the Alberta Wildlife Act. That remained in effect until 1987 when the act was amended by setting the 22nd baseline as a defining boundary for bison. The intent was to permit private ownership of bison in all areas south of the line. North of the line all bison were protected wildlife. Those areas north of the line included all areas where free-ranging bison were known to exist. This regulation made no distinction between wood bison or plains bison. The numbers of persons raising bison south of the 22nd baseline in 1970 were relatively few.

Around 1985, one individual imported 150 bison without permits to his farm near Fort Vermilion, well within the protected zone north of the 22nd baseline. A decision was made to amend the regulations to permit unrestricted ranching of plains bison rather than to lay charges against this individual. The act was amended in 1987 by deleting the reference to the 22nd baseline and excluding plains bison from the status of wildlife. Wood bison throughout the province were given full protection as endangered wildlife. This left "hybrid" bison outside Wood Buffalo National Park without a clear legal status. Although this occurred more as an oversight, it was several years before non-native hunters discovered this opportunity.

2. *Early Era (1772-1924) — Years of Low Numbers*

A. *Explorers, the Early Fur Trade and Researchers*

Samuel Hearne, the first European in the region, referred to bison as "very plentiful" (Hearne 1795) (Figure 6). In the company of Dene hunters, he killed a number of bison along the east side of the Slave River. Since then, explorers passed through the area throughout the 135-year period until about 1907. Unfortunately only a few of them recorded detailed observations of the abundance of bison (see historical reviews by Preble 1908, Raup 1933, Rich 1938, Soper 1941, Fuller 1966, Mitchell 1976 and Ferguson 1990a, 1990b). Bison were reported to be present as far north as the Horn Mountains (Figure 2). Other frequently mentioned locations are the Birch Mountains, Fort Liard area, Salt Plains, Hay River (possibly the Hay/Zama Lakes region), and Fort McMurray. The last area listed is of interest because, today there appears to be no suitable habitat for bison in that region. Important ranges for bison existed along the upper Peace River in the Grande Prairie area. Their presence there was first recorded by Alexander Mackenzie on his way to the Pacific coast. Further down the Peace River, and south of its junction with the Slave River, is the extensive Peace-Athabasca Delta, the largest inland delta in the world. Located at the eastern edge of the Delta is the village of Fort Chipewyan, and although not in the Park, the local native population has had close ties for centuries with the region that now contains the Park.

Fort Chipewyan is considered the oldest European settlement in Alberta and after its establishment in 1788, it rapidly became a major center of the fur trade. Other forts were soon to follow further up the Peace River, two of the major ones being Fort Vermilion and Fort Dunvegan. Ferguson (1990), in researching North-west Company (NWC) journals, suggests that Boyer's Post, a fort on the Peace River, was coeval with Pond's Fort along the Athabasca River and preceded Fort Chipewyan and related forts on the shores of Lake Athabasca. Clerks or chief traders in charge of these forts would maintain official records, which served as small, but important "windows" shedding some light on the conditions of the historical past.

A review of the records indicates that depletion of game populations (including bison) began some time in the 1800-1817 period (Ferguson 1990). From an historical perspective it is curious to note that Fort Chipewyan was considered a "fish fort" while the posts along the upper and central Peace River area were "buffalo posts". Knowing as much as we do now about the general productivity of the Delta, in terms of its carrying capacity as witnessed in the increases of bison during the post bison introduction period of 1925-1928, we could have expected that bison would have been far more common in the area than they appear to have been. It appears that right from the time of early European explorers, the main concentrations of bison were in aspen parkland, central and upper aspen parkland, prairie landscape of the Peace River country, and the Hay Camp area in the Park.

A Hudson Bay Company (HBC) reconnaissance team staying in the Lake Athabasca area in 1791-1792 reported that:

> It's from that River [Peace] that the Canadians [NWC] procure all their dried provisions for their different purposes, it's at the first settlement up the Peace River where they procure the provisions. I am informed that they go to it in fourteen days from the Athapiscow Settlement [Old Fort] ... [they] fetch down 2 Tons of Dried Provisions at a time and this Canoe keeps working most of the summer on purpose to supply the Athapiscow Settlement [Tyrrell 1934: 452, cited from T. Ferguson 1990].

In reference to the above, the "Athapiscow Settlement" being near Fort Chipewyan and the first settlement up the Peace River probably being Boyer's Post, i.e., Vermilion (T. Ferguson, pers. comm.). Why would the men go to Boyer's Post (14 days travel) if bison were readily available in the Peace-Athabasca Delta near Fort Chipewyan? This is one of the earliest indications that bison could not have existed historically on the Delta in the great concentrations that occurred during modern times. In fact, Phillip Turnor, part of a Hudson's Bay reconnaissance team, in surveying the region for future posts in the Lake Athabasca region in 1791/92 recommended that a provisioning post should be built along the rapids on the Slave River — a location north of Hay Camp (Tyrell 1934). Their report further identified the central and upper Peace River area as important bison areas. Again this indicates that the Delta was not an important area for bison in the fur trade era. Similarly, Mackenzie praised the central and upper Peace River areas as suitable bison ranges, but did not mention the Delta as a place to find large herds of bison (T. Ferguson, in prep). Could the 1791/92 observations, implying a low bison population in the Delta, be an artifact of earlier extreme hunting pressure? Given that the earliest post of the Fort Chipewyan area (Old Fort), was established just a few years previously, this seems unlikely. Could the residents of the even earlier Pond's Post (1785-1788) have been responsible for such a depletion? Not much information is available on Pond's Fort, but it is perhaps significant that in 1787, when an early freeze-up prevented a party from taking an outfit by canoe from Pond's establishment to the Peace River post, 12 men undertook a journey on foot to the Peace River "...in order to trade some provision for their canoes on their voyage out in the spring and to induce the Indians to come to the Fort with their hunt in March" (Lamb 1970: 431, Letter of 1 February 1788). In other words, Pond's Fort seems to have had a strong reliance on the Peace River for meat provisions too, again suggesting no substantial bison herds in the Delta area. It is not to be interpreted that bison were completely absent from the region of the Delta (Gates et al. 1992). Certainly many casual references are made to the presence of bison at various locations, but never in such terms as one would expect if the herds were as large as they have become in modern times.

According to Ferguson (pers. comm.), the subsequent historical records (1792 to 1840) make no overt references to bison diminishing in the Delta in the early 19th century. However, by the end of the 1820s, references to bison harvests pertain

to kills on the north bank of the Peace, or occasionally up the Athabasca River, but not in the Delta. Ferguson speculates that the disappearance of whatever bison did exist in the Delta may have been caused by overexploitation of a herd smaller than modern-day numbers. One such herd was reported as wintering at Lake Claire in 1820-1821. When the lake fishery failed in that year, the HBC and NWC posts at Lake Athabasca had to rely on the game harvests. The HBC post depended greatly on the bison at Lake Claire and perhaps the NWC post did too. The HBC clerk, Brown, wrote that the NWC post alone had harvested over 300 animals that winter, not all likely being bison as moose were also probably killed. The fur trade records appear to suggest that after the 1820s, bison in the Delta were essentially of no consequence for human food consumption. This is not evidence of their absence. For example, when the explorer Sir John Franklin passed through the area in 1820, he noted that there were numerous bison tracks near the post on Christmas day (Franklin 1836). Where were the sightings of large herds that one would have expected to see if they were present in large concentrations? Since 1820, most records also indicate that bison numbers were higher north of the Peace River, around present-day Salt Plains and Hay Camp. Further reference to bison in the Delta often pertains to sightings from the neighbouring Birch Mountains.

Evidence from 1840 to 1925 indicates that bison were still present west of the Slave River (MacFarlane 1908, Preble 1908, Seibert 1923, Raup 1933, Ferguson 1990). MacFarlane (1908) stated that during his 15-year residence (1870-1885) at Fort Chipewyan, hunters killed bison north of the Peace River every year. Raup (1933) stated that prior to 1873 more hunting took place north of the Peace River than anywhere else, and that "...further evidence that the region south and west of the present site of Fort Smith was the formal center of abundance is the fact that, in spite of its having been one of the areas most actively hunted throughout the years of decrease, it maintained the remnant herds longer than any other district".

It is not yet known whether bison occurred in significant numbers south of the Peace River, prior to the first intrusion of Europeans into the Fort Chipewyan area between 1778 and 1788, or, how abundant they might have been from 1778 to 1820. We want to stress and emphasize *significant* numbers — evidence of mere presence is not synonymous with their *presence in large numbers* i.e., comparable to herd sizes seen since the 1925 introduction. Nowhere south of the Peace River are bison mentioned as being present in large numbers. We recommend further search of the historical records because the absence of known records to date does not constitute proof of absence. Whatever comments about bison available for Fort Chipewyan often placed these herds at some distance from the Fort. During 1820, Simpson stated in his Hudson's Bay Journals (Rich 1938) that "Buffalo and Moose Deer are numerous in the neighbourhood — of Fort Chipewyan — say within four to six days in march of the establishment.". Simpson does not indicate in which direction these bison were found, or whether any river(s) had to be crossed to reach them.

One additional source of historical records of the status of bison in the Delta was to interview older trappers. Francois Gibot has trapped all his life along the northern edge of the Delta, along Sweetgrass Creek, and north to Lake One. His

father, born in 1910, also trapped in the area, as did his grandfather, born sometime in the early 1860s (F. Gibot, pers. comm.). By virtue of their lifestyle, traditional knowledge of the area is deeply rooted in this family. Throughout this time, when information was passed on from generation to generation, only one encounter with a bison south of the Peace River prior to 1925 could be recalled (interview with L. Carbyn 1986).

Scientists who worked in the Park in the first half of the 20th century relied on published information from surveyors and other scientists, but did not review the fur trade diaries. Raup (1933) concluded that "there appeared to be no appreciable reduction in numbers anywhere in the north until after about 1840." Between approximately 1840 and 1893, hunting by man (Ogilvie 1893, Raup 1933), and higher-than-average crusting of snow (Ogilvie 1893) and snow depths (letter from E.N. Nelson in Allen 1877, cited by Preble 1908; Ogilvie 1893) appear to have resulted in precipitous declines in the population. The population declined most rapidly within a 20-year period (Raup 1933); however, Ferguson (in prep.) discussed the implication of this observation in a broader context. Raup conducted range studies in the Park and commented on the population status of bison. His views of the bison declines in earlier years were based on a comprehensive review of journals by transient travellers and often involved second-hand reports from unspecified sources (Ferguson 1990). Raup suggested that the beginning of the most rapid decline occurred after 1860, while Ferguson (1990) suggested that the heavy dependence on meat by the fur trade, particularly in the context of fierce competition between trading companies in the 1800-1817 period, caused a depletion of bison much earlier. The latter hypothesis would appear reasonable for the region as a whole, but one would speculate that if such were the case for large herds within the Delta that the slaughter must have been massive and quick in order to account for the virtual disappearance of those herds for about 2 centuries. Possible, large-scale, rapid declines by hunting of bison in the Delta does not explain why remnant bison survived north of the river. Considering current declines (1971 to 1991), we speculate that two other factors might have contributed to low numbers of bison in the Delta, namely, increased vulnerability to wolf predation in open areas of high concentration and large-scale flooding which could have had disastrous consequences. Under this scenario one can certainly include increased vulnerability of bison to human hunting in the open delta areas, as opposed to more limited visibility in small ranges in forested areas, as an additional factor. Whatever the causes it will never be known how close to the brink of extinction these remnant northern herds were.

The numbers for the whole region apparently reached a critically low level late in the 19th century — at its lowest point during the late 1890s, the population was estimated at 150 to 500 animals (Ogilvie 1893, Preble 1908, Raup 1933) or about 500-600 (Hornaday 1889). During 1900, an Indian agent stated: "At Fort Chipewyan, Fort Smith and Fort Resolution I made close inquiries into the number of Wood Bison remaining, having an opportunity to do this owing to meeting so many Indians ... such as I think no one else has enjoyed ... herds which are ... three in

number: one ranging from Salt River to Peace Point on the Peace River, one from Salt River north to Great Slave Lake, and one from Salt River east and west. The number I conclude is from 500 to 575 head" (Preble 1908). It is likely that the herds in the Great Slave Lake area around 1900 were the only free-roaming bison left in Canada (Anon. 1926); the population of approximately 500 bison in that region represented about 60% of all bison (both wild and captive) that remained in North America at the time (McHugh 1972).

Ground surveys of bison in the subsequent management era began at around the turn of the century. Inspector Jarvis of the Northwest Mounted Police made the first extensive patrols in the region in 1897. During the subsequent years the Northwest Mounted Police assumed an increasingly active role in law enforcement and in obtaining information on bison numbers and distribution. In 1911, care of the bison passed from the police to the Superintendent of Forestry, and resident game guardians were appointed. Administrative headquarters were eventually established at Fort Smith in 1921, which preceded establishment of the Park by one year. Kitto (1924), in 1920 was assigned to survey the herds and make recommendations for a park. As an aside, it is of interest to note that Kitto suggested it was an indignity to the magnificent beast to be called a wood buffalo and not a *Bison americanus*. Seibert, also in the federal department responsible for Parks in 1922, was assigned to follow up Kitto's work and count the bison on the bison ranges. Seibert was later joined by Maxwell Graham. Graham counted 114 bison from a "Hochsitz" at the Salt River crossing and that is all the hard data that appears to be available (Fuller, pers. comm.). By autumn 1922, the two investigators felt that they were able to come up with an approximate figure (1,500 bison) on the general status of the bison north of the Peace River; no mention whatsoever was made for the range south of the river because it was known to be unoccupied.

B. *Mortality Factors*

i) Disease

Early observers did not mention disease in bison. If disease was present, it may have occurred at such low rates that major die-offs did not take place. Although diseased animals often cannot be diagnosed without clinical testing, W.A. Fuller (pers. comm.), who field-dressed numerous bison during the late 1940s and early 1950s, doubts that observers would not have commented on acute cases in which symptoms (e.g., lesions, bone abnormalities, etc.) were obvious. Again a closer review of historical information is recommended. Major die-offs due to disease in the 19th century were mentioned by native people during the 1990 FEARO panel hearings as possibilities (Ferguson and Laviolette 1992).

ii) Wolf Predation

Not much information on wolf predation on bison is available from the pre-1840 fur trade records (T. Ferguson, pers. comm.). Seton (1886) and West (1903, cited by Raup 1933) mentioned wolves, but little information on the number of wolves

or their impact (as predators) on bison is available from early records. Kitto (1924) stated "Wolves still prey to some extent on them, but except in cases where they manage to cut off a single animal do not inflict serious damage".

C. *Legal Protection*

As a result of a Senate investigation and Ogilvie's report, bison were granted legal protection in 1894, when the Unorganized Territories Game Protection Act was passed in parliament. Amendments to the Act extended protection until 1906, when the Northwest Game Act came into force. Little in the way of organized surveys was carried out either before or immediately after the introduction of laws protecting wood bison. Between 1897 and 1911, the police patrolled the area north of the Peace River; their initial efforts centered on enforcement (patrols and protection of bison), but they also recorded the abundance, distribution, and seasonal movements of bison. The involvement of the Warden Service developed, over time, from the law enforcement role of the Northwest Mounted Police. At first, game guardians (Buffalo Rangers) took over the responsibilities of law enforcement and surveys (1911-1922); these roles were later assumed by wardens (1922 to the present).

When Wood Buffalo National Park was established by Order-in-Council in 1922, it did not include the Delta, presumably because, historically, the latter had not been important to bison. The Park's original size was 26,800 km^2; it contained approximately 1,500 bison (Graham 1923), but the precise figure is not known. When plains bison were introduced (beginning the management era), most were released at a site 2 km north of Hay Camp on the Peace River (i.e., in the Park), but none were released in the Delta.

D. *Discussion*

We are not aware of any paleontological records of bison in the Delta that would indicate evidence of a prehistoric post-Pleistocene presence. Van Zyll de Jong (1986) and Geist (1991) discussed the possible evolutionary history of wood bison. North American bison populations once had a shared continuous distribution across to Asia. After the emergence of the Bering Strait at the beginning of the Holocene period, the Siberian population became extinct, but the American population survived and extended southward. Currently, there is renewed interest in evaluating the taxonomic position of plains and wood bison. Studies are in progress reviewing the subject. Nor do we have information on the seasonal movement patterns of the historical populations of bison in the region. Apparently migrations on the prairies further south took place between the more sheltered boreal parkland areas in winter and the open plains in summer (Moodie and Ray 1976, Morgan 1980). Specifics on these dynamics are not available, and how the predators adapted to such a system of a mobile prey population is open to speculation. One matter is quite certain — at no time in the historical past is there any evidence that bison in the Peace-Athabasca Delta were ever as numerous as they were in the mid to late 20th century (see earlier section). In contrast, one reference for the less travelled Slave River

Lowlands region (some 200 kilometres north of Peace-Athabasca Delta), noted that Peter Fidler, a surveyor, had seen large numbers of bison there in 1791 (Tyrrell 1934).

Why did bison in historical times not use the Delta to the same extent as they have in modern times? If populations were so reduced in one period the possibility should be that they would return sometime thereafter. Considering the richness of available bison habitat, it is difficult to imagine that the area could have essentially been without these ungulates for any length of time. One cannot rule out, of course, the possibility of bison having been common, but remained unreported. The likelihood of that must be considered remote because the fur traders' lives revolved around availability of game for survival.

Several explanations are possible. Conditions on the Delta may have been different from those of more recent times. However, it is doubtful that the Delta's vegetation or water regime prior to the arrival of European settlers could have been drastically different from the condition of these factors during recent times. At local sites, on a small to medium scale, the Delta is known to be in a constant state of change; however after reviewing the narrative of early explorers, Fuller and LaRoi (1971) concluded that its overall appearance has not changed much over the last 300 years.

Secondly, the habitat preferences of wood bison may have been different from those of plains bison — for instance, wood bison may have preferred small prairies interspersed with woodlands; whereas plains bison may have preferred larger, more open expanses. In addition, wood bison may have preferred woodland vegetation to sedges; the latter may have been favoured more by plains bison. There is no evidence to support these contentions; future studies in boreal forest areas particularly those currently being released into new northern ranges may provide data on the differential habitat preferences of northern bison. Experience in the Mackenzie Bison Sanctuary has shown that when conditions are ideal bison considered to have strong wood bison characteristics also use large meadows (Larter 1988), form large herds and certainly depend on sedges for survival in winter.

Because the virtual absence of substantial numbers of bison on the Delta during the early era has not yet been confirmed, the degree to which any impact of hunting by Europeans may have caused this decline is unknown. If bison were present heavy hunting might have resulted in their quick local extirpation and might partially explain their apparent absence from the Delta until the time that some of the introduced plains bison crossed the Peace River a century after the height of the fur trade. Excavation of a building near Fort Chipewyan (Nottingham House archaeological site, Karklins 1979) indicates that moose were an important food item of early explorers living in the area. If this is further substantiated by other archaeological digs, it would support the hypothesis that wood bison were less available on the Delta than in other areas and therefore, by implication, and moose enjoyed higher survival. Bison may have preferred the Birch Mountain area and an area north of the Peace River to the open Delta land south of the river. It should be pointed out that there was a 32-year period between legal protection and the

Photographs of bison slaughters in Wood Buffalo National Park. Top — young bulls shot and dressed in the field. Lower left — carcasses being winched onto a platform and transported to a portable abattoir during the early 1950s. Lower right — biologist William A. Fuller during the early 1950s, carrying out a field necropsy on a bison that was shot when test and slaughter was conducted and meat was supplied. Meat for human consumption was made available from 1929 to 1927 to the missions, prior to the time when meat was processed in commercially-operated abattoirs.

W. A. Fuller was the first investigator to carry out detailed research on the incidence of diseases in the bison population of Wood Buffalo National Park. This pole structure was used to hoist up remains of a calf, in order to examine how early tuberculosis will affect young after birth.

Bison roundup to control anthrax began in 1965 and this initiated a period of extensive construction of corrals and drift fences. The largest and most extensive roundup of wildlife in North America for disease control was carried out in the Park over a 12-year period. A total of 27,943 animals were handled, resulting in capture mortality conservatively estimated at 1-6% per year. Bison still walk through these structures, but they also function as barriers when they obstruct fleeing herds from escaping pursuit by wolves.

introduction of plains bison; ample time for bison to move into the Delta. It is conceivable that in wooded situations (typical of the area north of the river) bison were less vulnerable to hunting by both Indians and Europeans than they were on the Delta.

The heavy "human hunting" hypothesis needs further review. Given the known population of an excess of 8,000 bison in the Delta in the mid portion of the 20th Century, we would expect that in the absence of other mortality factors, such a population could only be reduced by man if hunting had been "excessive". A population of 8,000 bison probably consists of approximately 4,000 cows (older than 27 months), which theoretically could produce 2,000 calves annually. Because hunters would not normally kill calves, a population could have 2,000 animals removed, which would then be replaced by the annual calf crop. Biomass of such a productive system would amount to approximately 1,700,000 kg of live weight annually. It is highly unlikely that from the early days of the fur trade (when first records were kept), such a massive demand on the herds would be put on the population which would have resulted in a rapid decline. To produce a rapid decline would require removal of many more than 2,000 per year. There is no doubt that over time the fur trade could have exerted heavy pressures on local bison herds, and that in fact, appears to have been the case for some areas. For example, Simpson (see Rich 1938) in 1821 wrote about one post[1]:

> "Some few years ago, Buffalo were very numerous in the vicinity of the Establishment, but are every successive year retiring to a greater distance being continually hunted and are now rarely to be found within Six and Eight Days March of the Fort [Rich 1938:380]."

Human hunting pressures would be a result of the need for hunters to procure provisions for the fur brigades and meat for the forts. The number of people residing in the forts would be some indication of how much meat was required. In 1804 there were five Northwest Company posts and four additional posts in the entire Peace River area (Hudson Bay Company archives B29/a/3 as cited by T. Ferguson, in prep., entry 20 May 1804). In 1820, two posts in the Fort Chipewyan area registered 206 people (126 men, 31 women, 49 children plus some people for whom there was no accurate accounting). At Fort Chipewyan, meat was scarce, and fish was easier to obtain so meat was eaten only twice a week (T. Ferguson, in prep.). While in "the buffalo posts", 8-10 lbs of meat for a man, and half as much for a woman were considered the standard rations. According to Simpson's journal the post, around 1820, consumed about 90 lbs (40.4 kg) of meat (bison?) per day. Today the Fort Chipewyan population numbers about 1,200 people and the estimate of all

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1 Fort St. Mary 1817-1821 was located at the confluence of the Smoky and Peace Rivers.

"country food" consumption (of which meat is the greatest proportion) is approximately .5 kg per person per week (Wein and Sabry 1990).

Wood bison i.e., the northern bison, may have been poor dispersers, restricted to traditional ranges because of stereotyped migratory behaviour (an unlikely possibility), or may have been consistently exposed to a mortality agent in the Delta that was absent elsewhere. Any discussion of the factors that could explain what would appear to be the virtual absence of large herds of bison in the Delta during the early era would be purely speculative. Wolf predation, human hunting, winter severity, drowning, and disease all could have been important. One could, for example, speculate that if major ice jams had regularly occurred on the Peace River, thus flooding the Delta regularly, as was the case in 1974, conditions for bison survival in large numbers would have been impossible in earlier centuries. It should be pointed out that prior to construction of the Bennett Dam there were periods of 5-7 years when there was no flooding and then when flooding occurred in consecutive years. Possibly none of the above factors, either singly or in combination, was reason enough for the apparent low numbers of bison in the Delta. It is also possible that as their numbers increased over time, wood bison would eventually have crossed in greater numbers into the Delta after legal protection was applied in 1894.

The discussion of the status of bison in the Delta parallels a more general situation of low densities of all the bison in the north. In the conclusion reached by the FEARO panel it is stated:

> "It is clear that wood bison were never as numerous as those of the plains. One estimate placed their maximum number at 168,000. It is also clear that their decline was not due to over-hunting, as was the case with the plains bison. Exactly what factors are responsible for their brush with extinction are not well known. Several winters of unusually deep snow (up to 14 feet according to one observer) were mentioned in early accounts. Beyond that, we know nothing" (FEARO panel report 1990).

3. *Management Era (1925-1968) — Years of Increase*

A. *Introduction of Plains Bison*

This era began with the introduction of plains bison into Wood Buffalo National Park — the most significant single event in the management of the Park's bison population (Figure 6). Between June 1925 and July 1928, 6673 plains bison (4,826 yearlings, 1,515 two-year-olds, and 332 three-year-olds) were introduced south of Fitzgerald, a location that was reputed to be ideal bison range. In all "consignments", females were in the majority (Stevens 1954). The bison were shipped by train north from Wainwright, Alberta to Waterways, Alberta in cattle cars. At Waterways, the animals were transferred to scows and taken down the Athabasca River to Fort Chipewyan and then on to the Slave River where they were finally released in Wood Buffalo National Park. By 1926, some of the introduced bison

had crossed the Peace River onto the Peace-Athabasca Delta and inhabited that area from then on. In order to protect the bison south of the river approximately 17,408 km^2 were added to the Park in 1926.

The introduced bison were descendants of the "Pablo herd" (Anon. 1961) which was purchased in 1907 by the Government of Canada from Michel Pablo, a rancher near Missoula, Montana. This herd's origins dated back to approximately 1873, when an Indian captured four bison calves on the Milk River in southern Alberta; these calves were moved to the Flathead Indian Reservation in Montana. By 1884, the original four and their offspring formed a herd of 13, ten of which were purchased by Pablo. These animals and 26 from Nebraska formed the nucleus of a herd, some 716 of the descendants of which were purchased by the Canadian Government between 1907 and 1912. The 716 bison were delivered to the rail head at Ravalli, Montana for shipment by rail to Canada. The first year's shipment was released into Elk Island National Park, because fencing of the Buffalo National Park at Wainwright, Alberta had not yet been completed. Because they were fenced and protected at both locations, their numbers increased rapidly and by 1923 they numbered more than 6,600 head (Lothian 1976). Serious problems resulted from overcrowding at Wainwright, hence the official recommendation, after some debate, to release bison into Wood Buffalo National Park (Graham 1924).

After the transfer of bison from Wainwright was proposed, it was opposed by several conservationists. In an article published in the Canadian Field- Naturalist, reference is made to the opinion of well-known northerner, Charles Camsell, who, following a brief investigation of the bison ranges in 1916, suggested that there was no contact between the herds occupying the northern ranges (Nyarling River area) and the southern ranges (Hay Camp area). It was therefore assumed in official circles (Lothian 1976) that any integration of plains bison and the established population would be restricted to the Hay Camp area and that the northern herd would "remain inviolate so far as a mixture with the introduced bison is concerned." This notion was further supported when in 1963, northern bison were transferred on the basis that these were declared as essentially "pure" wood bison. A case was made that it would be unwise to allow either "hybridization" to occur or the introduction of diseases into the Park (Harper 1925, Howell 1925, Saunders 1925). It was also noted that wood bison, after being given legal protection, were increasing on their own — by the time the plains bison were released (Rowan 1929, McHugh 1972).

Despite the opposition, the government responded to the perceived needs of the time. Initially the Minister of the Interior claimed "...it is not the intention to mix breeds in any way", but it was soon apparent that hybridization did occur, giving Harvard zoologist, Thomas Barbour, reason to state that the transfer was "one of the most tragic examples of bureaucratic stupidity in all history" (McHugh 1972:306).

Roddy Fraser (pers. comm.), a resident of Fort Chipewyan, noted that those who had been involved in the transfer reported that "many" of the more than 6,000 bison may have died while in transit. He could remember as a boy going down to

the river and peering through the boards on the scows and seeing the bison packed "tight as sardines" on the boats. Further, Oldham (1947), stated that "...there is a wide difference of opinion as to the actual numbers that survived the trip; also, no accurate information is available as to the number of animals that succumbed shortly after arrival due to injuries sustained enroute as well as those that died due to change of site". These animals were shipped by railroad and crowded barges for a distance of about 1,100 km. Another description of the conditions of the animals was provided by Frank Laviolette, resident of Fort Smith. He noted on 15 January 1992 in a Canadian Broadcasting Corporation (CBC) radio program (excerpts available from CBC Toronto) that eye witness accounts by those who were involved in disembarking the bison found many to be in a weakened condition. Billy Schaefer was commissioned to shoot all those that appeared too weak to be able to survive (F. Laviolette, verbal presentation at the Northern Bison Management Board hearings, November 1991, Fort Smith). Local perceptions were that possibly as many as half of the animals shipped north never made it. Despite the losses, the conditions appeared to be ideal for those that survived and their numbers increased in the new ranges. By 1928, the total bison population was estimated at 7,500; it increased to an estimated 10,000 - 12,000 by 1934 (Soper 1941). Undoubtedly the introduced bison quickly mixed with the established population. Far more cows than bulls were shipped north. It is not unlikely that mature established wood bison bulls in the Park had a disproportionately greater influence on the breeding of young introduced cows than did the introduced plains bison bulls, which were mostly young animals. The infusion of this pool of plains bison genes (probably a less than 4:1 ratio) diluted the wood bison strain and stopped what was a promising comeback by the indigenous, northern bison population north of the Peace River. Because at the time of the introductions there were no, or very few, bison known south of the Peace River (as discussed in an earlier section), and movements to that region occurred soon after release, one could speculate that the genetic composition of the herds presently in the Delta is almost exclusively that of plains bison. However, observations (L. Carbyn, field notes) do not bear this out — bison on the Delta show many phenotypic characteristics of the wood bison as described by Geist and Karsten 1977. More sophisticated biochemical/ genetic-marker tests may be needed to quantify the degrees of hybridization if such a term is at all applicable in this context. When comparing the appearance of the bison near Fort Providence (Mackenzie Bison Sanctuary herd) with that of the Park's herds, one would expect greater variability in the latter because the Fort Providence herd originated from a small gene pool. More study, on both the phenotypic and genotypic characteristics of the bison complex in the Great Slave Lake area will be required to clarify these issues, but for the time being, it is our opinion, that Wood Buffalo National Park herds should not be discounted as inferior "northern bison" until further studies are carried out.

B. *Aerial and Ground Surveys*

Ground surveys of bison, just prior to the establishment of Wood Buffalo National Park (as discussed in the previous section), set the stage for the establishment of park boundaries. However, it was J. Dewey Soper, who from 1932 to 1934 lived and worked in the area, obtained the earliest information on the status of the bison herds after the reintroductions. He established "bench mark observations" on the status of wolves and noted that numbers were lower in early 1930. Soper returned to the Park in 1945 and found that wolf numbers had increased. It was Soper's report of the high wolf densities in the 1940s that precipitated renewed efforts to control wolves which lasted until the late 1960s.

The first recorded aerial survey was conducted during 1932, using a military aircraft. The first systematic survey was conducted during 1946/47 by the Park Superintendent (Oldham); at this time 2,494 bison were counted using a strip census at 1/6 coverage. Using the technique of spacing 3.2 km transects 12.8 km apart (1/4 coverage), Fuller counted 3,263 and 2,227 bison during 1949 and 1951 respectively (Fuller 1950, 1951). Using Fuller's technique, Novakowski (1957) counted 2,487 bison. Soper (1941) concluded that aerial surveys were inadequate because a large percentage of the animals (up to 80%) would not be documented if they were hidden by forest cover and, therefore, not visible from the air. Similarly, Fuller (1950) concluded from early survey efforts that bison numbers are underestimated when aerial surveys are used and overestimated by ground counts.

A new phase of aerial surveys began in the late 1950s and early 1960s, when the first total counts were made on the primary ranges in the Hay Camp, Lake Claire, and Conibear Lake areas (Novakowski 1961). In 1961, 10,273 bison were counted from helicopters and fixed-wing aircraft. Aerial surveys replaced all other kinds of surveys in the "decline era" (1969 - 1991).

C. *Mortality Factors*

i) Disease

It is difficult to assess the relative importance of disease and predation on bison numbers during the management era. Both factors were undoubtedly important and a brief review is relevant here. For a detailed assessment of the nature of the diseases, the reader is referred to reports by Broughton (1987) and Tessaro (1987).

Tuberculosis is an infectious disease of warm-blooded animals caused by a species of *Mycobacterium*. The bison at Wainwright tested positive for tuberculosis prior to being shipped to Wood Buffalo National Park (Lothian 1976). Therefore, tuberculosis was probably introduced to Wood Buffalo National Park during or after 1925, with some of the bison released into the Park (Fuller 1960).

Early protocol for the shipment north of the Wainwright bison called for tuberculin testing of all the animals. Later it was decided to forego this precaution. A decision to waive testing was apparently reached on the basis that older animals from the Wainwright herd were susceptible to disease and that if only younger

animals were shipped, there would be little or no chance of contracting the disease. This assumption proved incorrect. The bison that were released increased in the presence of the disease and in the presence of low wolf densities. Higher numbers of bison allowed for harvesting by man. Beginning in January 1929, bison were shot by hunters. The presence of tuberculosis was noted during some of the early slaughters (Mitchell 1976). Fuller (pers. comm.) noted that possibly the first confirmed record of a bison with tuberculosis was when an old bull staggered into Fort Smith and a medical doctor diagnosed it as tuberculosis. Testing of the bison in the Park was first carried out during 1947, at which time 8% of 52 animals necropsied showed lesions. By the 1950s, the number of bison killed had increased. Veterinarians and biologists who inspected the meat discovered high rates of tuberculosis in the slaughtered animals (Table 1), so the decision was made to use test and slaughter for disease control (W.A. Fuller, pers. comm.). The average rate of infection by one or both diseases between 1947 and 1974 was 28% [(range 4-47% (Park files)]; the rate of mortality from tuberculosis was thought to be approximately 2%, because that is the figure for generalized infections in the herd (Fuller, pers. comm.). In 1953, a plan was under consideration to eliminate tuberculosis by calling in the Canadian Air Force to annihilate all bison in the Park (W. Stevens, pers. comm.). Uninfected animals would then be used to repopulate the Park. This recommendation was made even before the outbreak of anthrax occurred (1964), or the presence of brucellosis was confirmed (1956) (see below).

It is difficult to determine the importance of tuberculosis as an immediate cause of death for a free-roaming population. The debilitating effects of the disease probably predispose bison to other mortality factors. Bison infected with tuberculosis can often survive for long periods and reach old age. However, the disease may weaken animals and reduce their mobility, especially when it is combined with arthritis, which is a common complication. Tuberculosis may also weaken cows to the point at which conception and calving rates are lower in infected animals than in disease-free individuals (Choquette and Stewart 1959). Conception rates were reported as being low in the 1950s (W.A. Fuller, pers. comm.). In addition, the disease undoubtedly made some bison more vulnerable to predation by wolves.

The presence of brucellosis, an infectious bacterial disease caused by a microbial species of the genus *Brucella*, was first confirmed in Wood Buffalo National Park during 1956 (Fuller 1966). Brucellosis causes a variety of symptoms in cattle, including blocked uteri, mummified fetuses, sub-functional ovaries, temporary sterility in both sexes (including orchitis, in which sperm count and viability are reduced), abortions (usually only in the first pregnancy), and reduced milk production. Presumably all of these symptoms are also found in bison. If brucellosis in bison produces sterility in bulls and/or causes abortions or influences mortality, it could have a major influence on a population's structure and numbers. The possibility is real that the effects of brucellosis on the population dynamics of bison may not be as great as has been suggested (for a review see Petersen, M.J. 1991). Female bison often have initial high abortion rates (up to 90%) during first pregnancy, but this drops to 20% at the second pregnancy and is almost zero in

Table 1. Prevalence of tuberculosis and brucellosis in bison in Wood Buffalo National Park, 1950-1981. (Compiled from Park files by S.V. Tessaro, R. Mitchell 1976). (L = lesions and R = reactors).

Year	Location	No. slaughtered	Tuberculosis		Brucellosis	
			No. examined	% infected	No. tested	% infected
1950/51	Salt Plains & Egg Lake	119	119	32.8 (L)	0	-
1951/52	Prairie River	218	218	19.7 (L)	0	-
1952/53	Hay Camp	245	245	45.7 (L)	0	-
1953/54	Hay Camp	276	276	46.0 (L)	0	-
1954/55	Hay Camp, 5th Meridian	21	21	40.0 (L)	0	-
1955/56	Hay Camp	205	205	27.4 (R)	11	27.3
1956/57	-	0	0	-	0	-
1957/58	Sweetgrass	450	1,065	14.5 (R)	200	35.0
1958/59	Sweetgrass	306	469	19.1 (R)	640	45.0
1959/60	Sweetgrass	457	1,116	13.5 (R)	155	38.1
1960/61	Lake Claire	126	126	46.8 (L)	75	53.3
1961/62	Sweetgrass	390	1,854	12.1 (R)	0	-
1962/63	Sweetgrass	67	67	41.7 (L)	0	-
1963/64	Hay Camp	159	155	40.0 (L)	0	-
1964/65	Hay Camp	152	152	18.4 (L)	143	13.3
1965/66	Lake One	0	0	-	0	-
1966/67	Hay Camp	162	162	30.9 (L)	161	15.5
	Hay Camp	337	337	38.9 (L)	337	22.2
1967/68	-	0	0	-	0	-
1968/69	-	0	0	-	0	-
1969/70	Fort Smith	9	0	-	0	-
1970/71	Sweetgrass	197	197	25.4 (L)	164	39.6
1971/72	-	0	0	-	0	-
1972/73	-	0	0	-	0	-
1973/74	Sweetgrass	114	114	21.1 (L)	113	61.9

subsequent pregnancies (Davis et al. 1991). The dissemination of brucellosis, like that of tuberculosis, is facilitated by the gregarious nature of the host. The disease is transmitted primarily by oral contact with contaminated placenta, blood discharges associated with parturition and with aborted fetuses. Positive reactors to tests have varied from 3-62% (Mitchell 1976 and Table 1), with an average of 33%. Brucellosis may or may not have been introduced into the Park with the plains bison. However, all the evidence strongly suggests that the presence of both diseases is a direct result of the introductions.

Anthrax is caused by the bacterium *Bacillus anthracis*, the spores of which are known to retain their viability in contaminated soil for more than 60 years. In North America, the disease is believed to date back to the early 1700s, when it may have been brought from France in livestock by immigrants who settled in Louisiana (Cousineau and McClenaghan 1965). The first outbreak of anthrax in the Wood Buffalo National Park area occurred at Hook Lake, N.W.T., during 1962 (Novakowski et al. 1963); the first outbreak within Wood Buffalo National Park occurred during 1964. Between 1962 and 1971, a minimum of 1,003 bison from the Hook Lake and Wood Buffalo National Park herds died of anthrax (Choquette et al. 1972).

How anthrax reached the bison in the Park is not known. It may have been endemic to the Park and may have caused declines in the wood bison population during earlier years, or the disease may have been introduced into the area by outfitters' horses that were used in the Hook Lake area during the early 1960s. However, anthrax is highly virulent in horses, so it is doubtful that the disease was introduced by this route (S. Tessaro, pers. comm.). The most probable source is migratory birds that visit certain areas in the United States in which anthrax is believed to be endemic (E. Broughton, pers. comm.). Susceptibility to anthrax may be associated with gender; of the 48 victims of anthrax in Wood Buffalo National Park during 1978, 42 were male, two were female, and four were of unknown gender (Park files). The reason for this gender-associated susceptibility may be behavioral (Novakowski et al. 1963). During dry years, spore dissemination is enhanced; spores may enter the respiratory system from dust clouds created when bulls paw and roll in wallows. In addition, avian and mammalian scavengers feeding at anthrax-infected carcasses probably serve as dispersal agents for the spores (Choquette and Broughton 1967). Currently it appears that anthrax in the Park is well established, and outbreaks can result whenever conditions are suitable.

The above summary implies that anthrax was not brought in with the introduction of plains bison. Although the record is not entirely clear, there is a strong suggestion that tuberculosis and brucellosis were introduced with the bison shipments from the south. Alternatively, both tuberculosis and brucellosis may have been endemic, but uncommon. Neither tuberculosis nor brucellosis results in observable die-offs, so if they were present prior to the introductions, the symptoms would not necessarily have been noticed. W.A. Fuller (pers. comm.) believes that the emaciation, pus-filled lymph nodes, and putrid smell found in animals with advanced cases of tuberculosis would have been noted, as would the enlarged testes

and arthritis associated with brucellosis, further supporting the suggestion that both diseases were introduced with the release of infected plains bison in the Park.

ii) Vaccination Programs

Programs to vaccinate bison against anthrax began during 1965, shortly after the first outbreak of the disease in the Park, and continued until 1977 (Table 2); between 1965 and 1977, 27943 (see Tessaro, Table 10) bison were vaccinated. Bison were

Table 2. Anthrax vaccination programs in Wood Buffalo National Park, 1965-1977.

Date	Location	Animals handled	Animals vaccinated	Known deaths attributed to roundups[1]
March 1965	Sweetgrass	1623	1547	18
March 1965	Hay Camp	Unknown	249	Unknown
May 1965	Lake One	2123	1507	111
September 1965	Hay Camp	Unknown	179	Unknown
October 1965	Hay Camp	Unknown	109	Unknown
February 1966	Sweetgrass	1455	1414	41
June 1966	Lake One	3587	2173	Unknown
June 1968	Sweetgrass	Unknown	210	Unknown
July 1968	Sweetgrass	Unknown	744	Unknown
July 1969	Sweetgrass	Unknown	3021	Unknown
February 1970	Sweetgrass	Unknown	595	Unknown
June 1970	Sweetgrass	3921	2857	44
June 1971	Sweetgrass	947	779	18
June 1972	Sweetgrass	4817	3612	326
February 1973	Sweetgrass	1084	1056	7
June 1973	Sweetgrass	3463	2887	16
June 1974	Nil - High water levels at Sweetgrass			
June 1975	Sweetgrass	386	337	3
June 1976	Sweetgrass	1110	933	17
June 1977	Sweetgrass	648	546	8

[1] Actual figures were probably higher, since some injured animals succumbed after release.

Source: Millette and Sturko (1977).

rounded up in large numbers and corralled at three locations (Hay Camp, Sweetgrass, and Lake One). L. Flett, an employee of the roundup operation at the time, told us of an incident where some 4,000 to 5,000 bison were herded from the Delta to Lake One. It took several days as the move was conducted in a way to least stress the animals. Human handling (roundups, corralling, vaccination) proved to be stressful to bison (Hudson et al. 1976). The impact of these activities could be physical (injury inflicted during handling in chutes, loss of calves caused by trampling, separation of calves from cows, goring by bulls) and/or physiological (stress-related myopathies, increased risk of abortion). The average recorded mortality for the animals vaccinated between 1964 and 1974 was 2%, with a high for one year (1972) of about 7% (Millette and Sturko 1977). Wardens believed that only a small proportion of the stress-related deaths were observed, so that the actual mortality rate was probably much higher than the recorded rate. If considerable numbers of animals died, either as a direct result of roundups or from secondary causes (including a potential increase in calf mortality), the vaccination programs could have had a significant effect on bison numbers, especially when combined with other stresses on the population. As will be shown in a later section, the end of roundups for anthrax control roughly coincided with completion of the Bennett Dam and the phasing out of wolf control operations. It should be noted that not all bison in the Park were subjected to vaccination.

iii) Slaughters

After the introduction of the plains bison, during a period in which the Park's bison population was initially increasing by natural means, the production of red meat for human consumption became important. Harvests of bison began in 1929 and continued until 1974 (Mitchell 1976). Initially bison kills for human consumption began on a small scale in response to Catholic missionaries who suggested that "...quantities of dried buffalo meat, when available, be placed at the disposal of the residential school" (pers. comm., P. McCormack as extracted from Park files). Control over hunting and meat distribution was in the hands of the Park administration. Sport hunting for profit, although proposed in 1931, was never sanctioned in the Park. Thus bison were on the one hand considered to be both a natural heritage worth preserving, and on the other hand a resource for human consumption. During the 1950s and 1960s, government administrators and society saw no conflict between promotion of the local economic gains realized by slaughtering bison to provide low cost meat to Northerners and the promotion of the Park's original mandate, namely, the preservation of the species. No provisions were made for ecosystem management and protection.

Numbers of animals slaughtered to provide meat for the Roman Catholic missions and Indian Affairs between 1929 and 1950 are summarized in Figure 6. Those kills were localized and not extensive, and the effects on total numbers compensated, to some extent, by simultaneously carrying out wolf control. Originally, bison for the missions' use were shot and dressed in the field. It was a progressive evolution of events that made greater use of the available resource.

Fuller's recommendation for test and slaughter was for disease control. Commercial profit of meat utilization followed in order to take advantage of the resources. The efficiency of the slaughters was increased in 1952, when portable abattoirs were first used to enhance handling of meat. At that time involvement by the Mission staff was discontinued (Tessaro 1987). In the first winter, 1951-1952, 218 bison were killed. Meat inspection was the responsibility of the Department of Agriculture. Slaughtering was carried out by the Park's staff, and scientific expertise was provided by the Canadian Wildlife Service. The portable abattoir consisted of three cabooses towed by a caterpillar tractor, but these were considered inefficient for processing bison (Fuller 1952). For example, approval was given to kill 400 animals, but only 218 were taken (Mitchell 1976). Wing fences and corrals were built to increase effectiveness of field-slaughtering bison in the Hay Camp area.

An abattoir was built at Hay Camp during 1954. The operation of abattoirs became more efficient and about 200 to 1,000 bison were killed per year. This was a result of shifting from hunters in the field (had a limited range) to hazing bison into holding corrals. Slaughtering ceased during 1956-1957, while a modern abattoir was being built in the Sweetgrass area (Olson 1958). Between 1958 and 1963, the control of tuberculosis and brucellosis became an important consideration, so animals were tested at abattoirs (Table 1). Meat was used for human consumption when tested to be safe. The Sweetgrass facilities were subject to flooding, which occurred in 1958, 1960 and 1962. A more modern facility was built at Hay Camp during 1961-1962 and used continuously until 1967. The last slaughter of 114 animals was approved during 1974. The last commercial slaughter at the Hay Camp abattoir coincided with Canada's Centennial celebrations (1967) when bison meat was shipped to Montreal for Expo '67. The demand for meat for local consumption continued, so slaughters were carried out in 1971 and 1974. Approximately 2,700 bison were killed between 1950 and 1959 and approximately 2,200 were killed between 1959 and 1974 (Park records).

iv) Drowning

Until completion and closure of the Bennett Dam, periodic floods caused extensive drownings. The only major flood after dam construction was in 1974. Bison may drown primarily during the "shoulder" periods — just after freeze-up and just before breakup — (for example, during spring or fall, when crossing thin ice on flooded meadows and rivers) because, unlike moose, they cannot haul their large bodies out of water and onto ice, and so become easily trapped. Local trappers have observed that bison also drown as a result of being swamped by waves while swimming across large lakes (A. Simpson, pers. comm.). Major drownings were recorded during the spring of 1958 [approximately 500 animals (Fuller 1966)] and the fall and winter of 1969 [between 1,703 and 3,000 animals (Olson 1961, Novakowski 1961)]. During 1962, meadows were flooded, but no drowinings were recorded (Olson 1962).

D. *Management Programs And Proposals*

In addition to the long-term management programs directed toward reducing disease and increasing the meat supply for human use, two other programs of note were implemented during the management era, namely, the wolf control program and the transfer of wood bison from Nyarling River (Needle Lake) to the Mackenzie Bison Sanctuary. The re-establishment of wood bison as a "pure" subspecies in Wood Buffalo National Park was considered in 1968, but not implemented. In many respects, this plan was similar to some of the options presented during 1988 in the report of the Disease Task Force. A summary of all management plans relating to bison in Wood Buffalo National Park is given in Table 3.

i) Wolf Control

Wolf populations were considered "low" during the 1920s (Fuller and Novakowski 1955); they appeared to begin to rise around 1925, and by 1932-1934, wolves were more numerous in the Park (Soper 1945). However, throughout the 1920s and 1930s, wolf numbers were considered to be much lower than in the 1940s (Soper 1945). Some evidence that wolves were low was given by Fuller and Novakowski. They stated "...this is given proof by the failure of the Wardens of the day to take many wolves even though they were permitted to retain the bounty on all wolves taken by them". Soper believed that, although predation on bison was noted, a greater proportion of the wolves were in the secondary bison ranges. Soper considered wolf increases to be part of what appeared to be a circumboreal trend that extended from Alaska to Ontario. Soper also believed that wolf predation on bison was a significant mortality factor in the 1940s, and along with other field workers expressed concern over the Park's increased wolf population, recommended that wolves be controlled in order to save bison, and thus increase the amount of meat available for human use (Soper 1945).

Buffalo Rangers started to poison wolves some time after 1935 (Mitchell 1976). Little information is available on how many wolves were culled; however, the program was probably effective in reducing the predation pressure on bison. Fuller and Novakowski (1955) stated that a decrease in numbers was apparent as no mention of wolf problems was made until 1941-1942, when renewed poisoning began.

Prior to 1935, wolves were controlled by hunting and trapping; a practice that has continued until today. The intensity of predator control programs varied. It is difficult to determine actual numbers killed, as there often is disagreement between reports, files and publications. In the minutes of the meeting of the Advisory Board on Wildlife Protection held on 3 August 1940, the following figures on the numbers of wolves killed were given: 1936/37 - 12; 1937/38 - 20; and 1938/39 - 26. The numbers of wolves killed as a result of control programs are not known (many wolves that were killed went unrecorded). What little data is available is as follows: 1941/42 - control program was in effect, but numbers not available; 1944/45 - 66 (Soper 1945); 1948/49 - 31 (Mitchell 1976); 1951/52 - 59 wolves were taken that

Table 3. Summary of management plans relating to bison in Wood Buffalo National Park.

Plan	Purpose	Fate
1893 - Legal protection followed N.W.T. Council Ordinance, 1897.	Protect a critically low remnant population.	Legislation passed but little enforcement.
1897 - Enforcement.	To enforce legal protection of bison by Northwest Mounted Police.	Northwest Mounted Police assigned to enforce bison protection 1897-1911.
1911 - Buffalo rangers.	Protection for bison.	
1925-1928 - Plains bison introduction.	To establish new bison ranges and relieve over-crowded conditions in Wainwright Buffalo Park.	6,673 bison were transported.
1929-1954 Bison slaughters.	To supply meat for human consumption.	Small number of animals were harvested.
1955-1974 Bison slaughters.	Test and slaughter for disease.	Continued to 1974.
1935-1940 - poison first used by Buffalo rangers to control wolf population.	Increase bison for human use.	Wolves poisoned periodically until the 1960s.
1953 - Proposal to annihilate diseased bison (in the whole park).	To eradicate tuberculosis from the herds using the R.C.A.F.	Preliminary discussion phase only - no follow-up.
1954 - Hybrid bison management plan.	To manage bison for aesthetic and economic reasons.	Plan followed up.
1962 - Wood Bison rescue plan.	To establish Wood Bison herds separate from Plains Bison hybrids.	77 and 47 bison were captured during 1963 and 1965 respectively, and formed the nucleus of various herds.
1963 - Nyarling Wood Bison transfer to Mackenzie Bison Sanctuary.	To rehabilitate and protect Wood Bison.	Introduced herd remained and numbers increased rapidly. A very successful venture.

Table 3. Continued.

Plan	Purpose	Fate
1964 - Anthrax control and detection program followed by a vaccination program during 1965. Activities were controlled by a multi-agency committee.	Search for and destroy cadavers, vaccination of bison.	Program was in effect until 1977 (because of flooding, program was not carried out during 1967 and 1974).
1968 - 5-year plan to fence or eliminate all free-roaming bison.	To produce a disease-free (tuberculosis, brucellosis) herd.	Plan was rejected because of cost and on environmental (aesthetic) grounds.
1972 - modification of 1968 plan - increase vaccination.	To increase number of bison vaccinated against anthrax; objective was to spread out number of corral facilities.	Rejected because of difficulty in vaccinating large percentage of animals, losses of animals during roundup, high cost. Roundup efforts increased for existing facilities.
1977 - eliminate anthrax vaccination.	Counter public criticism of losses due to roundups; save money on what was perceived to be an ineffective program.	Plan accepted.
1985 - Wood Bison Advisory Group, eventually becoming the Wood Bison Recovery Team - status report in 1987.	To review Wood Bison rehabilitation projects and provide advice on Wood Bison management to the Western Wildlife Directors.	Recommended in 1987 that Wood Bison be reclassified from "endangered" to "threatened", for commercial use of Wood Bison.
1986 - Task Force on disease control.	To review options for disease control.	Completed a report in 1988 and submitted material to an interjurisdictional steering committee.
1989 - Environmental Assessment Panel.	To hold public hearings.	Report submitted 1990.
1991 - Minister of Environment established the Northern Bison Management Board.	To recommend to the minister future course of action.	June 1993 - decision still pending.

year in Area I (Pine Lake to Salt Plains) from an estimated pre-poisoning population of 85 wolves (Fuller and Novakowski 1955); 1952/53 - 33; 1953/54 - 92[2], 1957/58 - 56; 1958/59 - 21, and 1959/60 - 19 (Park files).

We are not aware of the numbers of wolves killed in the years not listed above; however, it is believed that this information may be available. In a memo by E. Kuyt (Park files — 6 March 1973), further information on wolves killed in the Park was summarized.

Predator control continued at various levels of intensity until the 1960s. It appears that the exact date that they were terminated is not recorded. During the 1960s, control became more of a secretive operation as the environmental ethics of predator control became more suspect. Again, some kills throughout this period went unrecorded and were not always sanctioned by Park authorities. It is believed that, between the early 1940s and the mid 1960s, 20 to 120 wolves were killed per year. The largest number were reported as having been killed during the three-year period between 1951 and 1953, when at least 195 wolves were taken and again 1958 to 1960, when a minimum kill of 98 wolves was registered. After poisoning programs were stopped, wolves continued to be killed either as a part of deliberate efforts to obtain fur, or as a result of casual encounters with trappers. Official predator control was replaced (year not known) by regular wolf harvests of trappers, which resulted in a less systematic reduction in numbers. In 1967, local residents requested that wolf control be continued, but this was turned down by the Park Superintendent. Strychnine was still occasionally used unofficially in 1968/69. E. Kuyt found a coyote poisoned near Sweetgrass station in December 1968, and several cases of poisoning of sled dogs were reported in the Hay Camp area (E. Kuyt, Park files).

ii) Nyarling River — Mackenzie Bison Sanctuary Transfer

Geographically, bison in North America have been placed into two categories. Wood bison occupied the northern range, while plains bison were in the remaining North American ranges (Figure 7). It is generally accepted in management documents that the last herd of wood bison was discovered in the Nyarling River (Needle Lake) region during an aerial survey in 1957; however, W.A. Fuller (pers. comm.) and others had known about this remnant herd for some time prior to their discovery. The circumstances regarding the isolation of this herd require closer scrutiny.

Whether or not wood bison is a distinct entity (subspecies) from plains bison has been debated at length. Rhoads (1897) was the first to formally describe the subspecies. He admitted that the reports about differences were not always precise, but in general he concluded that wood bison were "larger, colours darker, horns

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2 Eighty wolves were poisoned at one location along Lousy Creek.

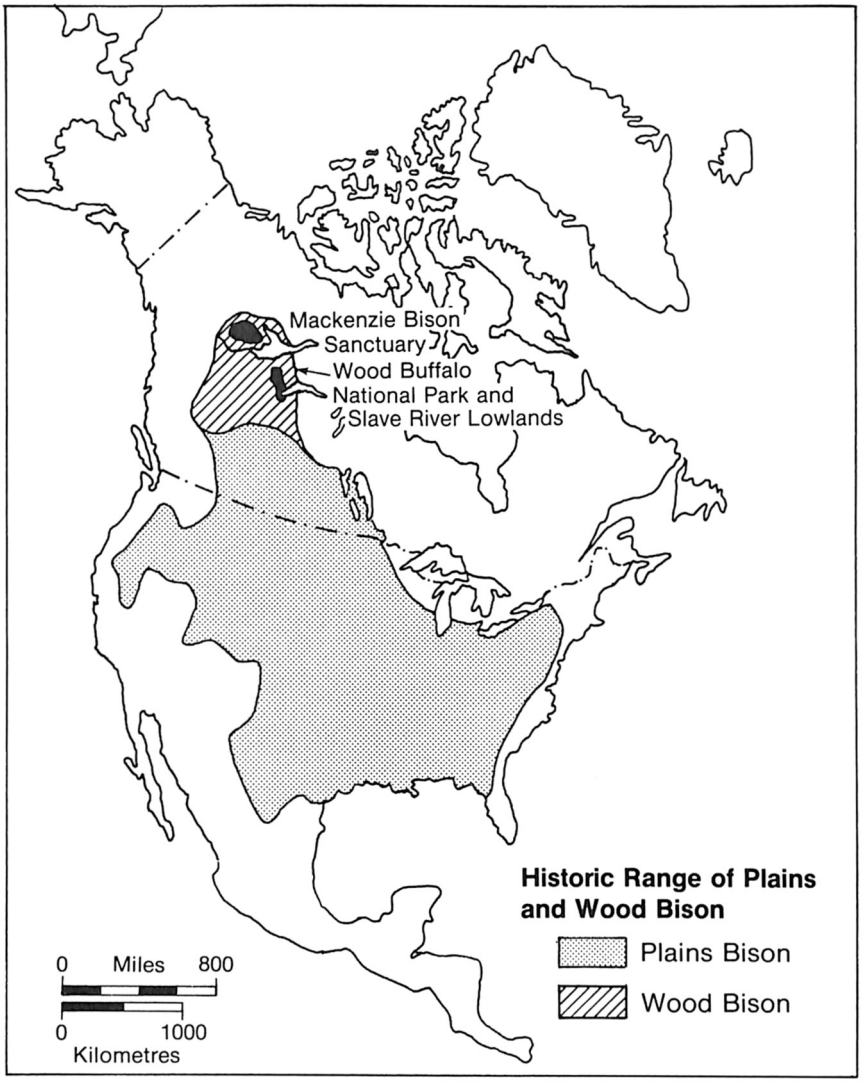
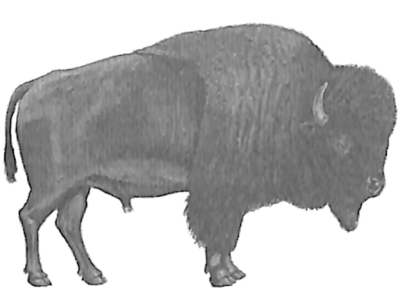
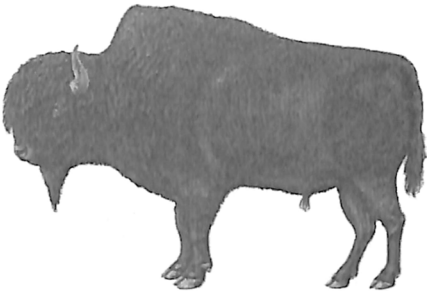


Figure 7. Historical distribution of bison in North America.

slender, much longer and more incurved and hair more dense and silky than the prairie bison." More quantified descriptions were rendered by Geist and Karsten (1977) and their descriptions became the archetype of the phenotypes upon which the wood bison recovery program was established. An artist's rendition of the differences are shown in these two examples (sketches reprinted with permission of Canadian Parks Service).



Plains Bison



Wood Bison

Plains bison appear smaller and stockier than wood bison. The most important differences appears to be related to body conformation. Wood bison have a taller and squarer hump, and are darker in colour. In summer, the cape of the plains bison has a more distinct boundary with the rest of the body and the wood bison have smaller, more pointed beards. These are considered the main differences, however, there often are wide latitudes in variations of the different features among individuals.

In 1991, the Taxonomy Subcommittees of the Wood Bison Recovery Team reviewed the criteria and refined phenotypic character descriptions into 7 categories. These being:

1) hump shape
2) cape demarcation
3) chap hair
4) frontal display hair
5) ventral neck mane
6) beard
7) cape variegation

Prior to the introduction of plains bison in the Park, Graham (1924) estimated that about 500 bison inhabited the northern range. They were separated from the southern range, with some likelihood that movement occurred between the two ranges. The discovery of the Nyarling River herd supported earlier speculation by Raup (1933) and Soper (1941), who thought that there must still have been what they believed to be herds of "pure" wood bison in the northwestern portion of the Park farthest from the points at which plains bison had been released. Seventy-seven of the remnant wood bison from the Needle Lake area were driven into a corral in February 1963. Sixty-one were tested for brucellosis and tuberculosis, two were not tested, and 14 developed capture myopathy (Novakowski 1963). Eighteen of the originally-captured founder herd were transported by barge down the Slave River, across Great Slave Lake, and along the outlet of the Mackenzie River to Fort Providence. Sixteen survived and were released 25 km northeast of Fort Providence.

These bison remained in the area and the population increased exponentially with a doubling time of three years (Fuller and Hubert 1981). The region was later set aside as the Mackenzie Bison Sanctuary. Of the estimated 3,000 bison considered by the Wood Bison Recovery Team as having wood bison characteristics, approximately two-thirds are free-roaming in the Mackenzie Bison Sanctuary (Gates and Larter 1990). This does not include bison from Wood Buffalo National Park that up to 1990 were considered hybrids and in need of replacement because they were diseased.

A second roundup occurred at Nyarling River during February 1965 (Novakowski and Stevens 1965). Twenty-four of 47 animals from this capture were held in Fort Smith; 21 of them survived the transfer to Elk Island National Park where they were used as breeding stock for wood bison rehabilitation projects in Jasper National Park, northern Alberta, the Northwest Territories, Manitoba, and the Yukon (see section iii). By 1968, three more calves had been shipped to Elk Island National Park from holding corrals near Fort Smith (one in 1967, two in 1968).

The entire wood bison program is based on a founder population of 37 animals, and three calves later born from diseased mothers in the Fort Smith corrals, all of which originated from the Nyarling River area in Wood Buffalo National Park. This founder population was considered to be isolated from the descendants of the introduced bison by approximately 160-320 km of karst topography, swamps, and muskegs (Banfield and Novakowski 1960). These authors state:

> "There is an intervening area of extremely inhospitable and unproductive terrain of karst topography, poorly defined drainage, and much muskeg interspersed with high sand eskers in the Ninishith Hills, which offers little inducement to migration or movements out of the Nyarling River area. These bison are therefore separated by distances of about 100 to 200 miles from the hybrid Hay Camp and Lake Claire herds and about 75 miles from the Grand Detour herd."

Earlier investigators failed to evaluate the map from the aerial survey conducted by Fuller during 1949 (Fuller 1950), which clearly showed that by the late 1940s the "southern" bison were not separated from "northern" herds by 160-320 km (Figure 8). Some degree of separation of herds probably only existed between major population clusters during times of low density. It is apparent that during the late 1940s (a time when the bison population was near its peak) the animals were distributed on patches of suitable range throughout the southern, eastern, and northeastern portions of the Park. At the same time, large areas existed without any bison, probably because of a lack of suitable range, particularly in the northwestern portions of the Park. Examination of the points plotted on Fuller's map shows that on a route from the Hay Camp area to Nyarling River no individual bison was farther than roughly 16 km from its nearest neighbour and that a continuum of bison extended from one area of concentration to another. Therefore, it is misleading to stress the distances between populations. Most genetic interchange probably occurred within the areas of greatest concentration, with some drift across the continuum. We believe, as have others (e.g., Van Zyll de Jong 1986) that this would have resulted in some infusion of plains bison

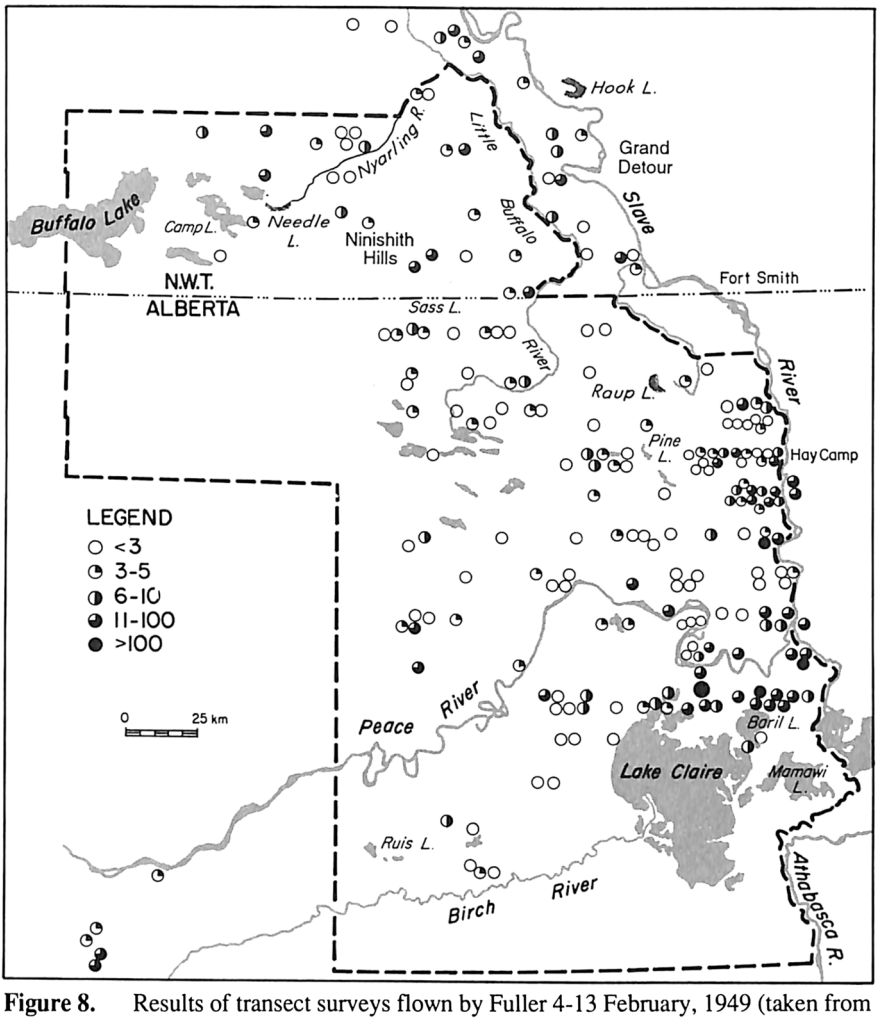


Figure 8. Results of transect surveys flown by Fuller 4-13 February, 1949 (taken from survey maps).

genes, but it is likely that wood bison genes were predominant in the Nyarling River herd. Evidence discussing the validity recognizing wood bison as a taxonomic category (subspecies or geographic race), that is physically distinct from plains bison, is provided by reviews in Geist and Karsten (1977) and Van Zyll de Jong (1986) and subsequently discussed by Geist (1991) and Strobeck (in progress). Currently, radio-tracking studies of bison in the Needle Lake area is providing new information on seasonal movements of the northern herds in the Park.

Five other lines of evidence support the hypothesis that contact between isolated bison in the Nyarling River herd and southern herds could have been more wide-

spread than was originally believed. First, bison are known to stampede and run for long distances when pushed by predators. For example, during February 1981, one of the authors (Carbyn, field notes; 1992) recorded a movement of 86 km by a herd of 90 animals. This herd had been attacked by wolves at Raup Lake and ran for 4 km before a calf was killed and eaten by wolves. The herd continued to run for 20 km through open forests and then ran for another 62 km on a ploughed road. They were later seen resting near the Cherry Mountain fire tower. The distance this herd had travelled was determined from an airplane by following their tracks in the snow; the entire distance had been travelled in less than 12 hours. H. Reynolds (pers. comm.) noted that in the Hook Lake area, bison often moved up to 32 km over a short period of time for no apparent reason. Second, bison captured in the Nyarling River area during 1963 and 1965 were not free of disease. Thirty two of 61 bison at Needle Lake either tested positive for diseases, implying that, if one assumes tuberculosis and brucellosis were not present before the introductions, mixing of the groups had occurred and/or was occurring (Reynolds et al. 1982). Third, apparently old, well-worn bison trails connect the north end of the Park with the Salt Plains, and therefore connect the areas of high concentration at Hay Camp and the Delta with those in the north.

Soper (1945) substantiated the claim by natives that the herds from the main bison herds ranged to the northwest. His quote is as follows:

> "Upon reaching the high country west of the Salt Plains, fresh signs became relatively common. Scattered individuals and clans were occasionally seen from Lobstick Lake across the Sass and Klewi Rivers to the headwaters of Nyarling River. In some areas, trails and other signs were plentiful. It has long been known that some of the Northwest Territories part of the Park constituted important summer bison range. At this time, I was traversing a section of country which I had not seen during the summer months of my previous two-year period in the Park. I was agreeably impressed with the amount of trails and the abundance of wallows and rubbing trees spoke eloquently of wide-spread occupation.The major part of the territory traversed to Nyarling River is well suited to the species at this season.....
>
> On this journey, I definitely established the fact that bison range northwest in the Park, during the summer, at least as far as the area drained by the headwaters of Nyarling River."

Fourth, through normal movements, bulls are known to travel long distances and then return. Studies currently in progress at the Mackenzie Bison Sanctuary have shown that such movements occur (Gates et al. 1992). A fifth source of evidence comes from an analysis of progeny that originated from the founder population (Van Zyll de Jong 1986). Evaluation of the range of phenotypic expressions indicated some strong affinities to plains bison in those animals captured at Nyarling River. In fact, one mature bull characterized as having strong affinities to plains bison was used in the wood bison rehabilitation program (See plate 2 — photograph 5 on page 44, Van Zyll de Jong 1986).

The mixing of groups does not rule out the possibility that bison in the northern part of the Park have stronger affinities to "wood bison-type features" than to

"plains bison-type features". A subjective comparison of the gross appearances of the Nyarling River bison with that of the bison observed at Lake One south of the Peace River indicates that differences in physical appearance seemed to exist (Carbyn, May 1981 field notes). However, this conclusion was made on the basis of non-quantified observations of small samples of bison seen in the north versus large herds seen in the Delta. Similar superficial impressions that were not quantified were obtained in the spring of 1990, while observing bison in the Mackenzie Bison Sanctuary (Carbyn, May 1990 field notes). It does appear though, that many of the bison observed in the Delta, particularly mature bulls, bear a marked physical resemblance to what in the literature has been described as wood bison. This leads us to question whether bison throughout the Park could not be considered bonafide wood bison or just simply northern bison.

Regardless of the degree of genetic "contamination" in the bison at Nyarling River, two groups of this population were moved to the Mackenzie Bison Sanctuary and to Elk Island Park. These bison became an important source for the reintroduction of wood bison in northern areas. However, we view the statement that pure wood bison exist in the Mackenzie Bison Sanctuary to be misleading and simplistic. The appropriateness of such a term in this context is questionable. "Purebred" is an agricultural term which has occasionally been mistakenly applied to the bison in the Mackenzie Bison Sanctuary by officials in Agriculture Canada and others. Also, it may well be that the bison in Wood Buffalo National Park have stronger affinities to wood bison than is implied by the sweeping, all-encompassing term "hybrid" population. Genetic research currently in progress may shed more light on the subject, Bork et al. 1990 and Strobeck (in progress). An analysis of phenotypic characteristics of various bison populations on the North American continent by the wood bison recovery team will be of importance.

The bison in the Mackenzie Bison Sanctuary have increased from 1963 to 1987 at an exponential growth rate of $r = 0.215$. During that period of time there was no evidence of wolf predation (Carbyn 1969, field notes; Calef 1984; A. Look, pers. comm. 1990). During the first hunting season, in 1987/88, four bison from a quota of 20 animals were killed by hunters. Twenty bulls were killed in 1988/89 when the quota was subsequently increased to 40 bulls. Wolf predation was soon noted after 1987 (Gates, pers. comm.) and has since been an important mortality factor.

(iii) Wood Bison Recovery Program

The Wood Buffalo National Park bison population provided the impetus for the northern bison recovery program. Once transferred from the Nyarling area, the seed stock for future releases were available for several reintroduction programs. Major transfers from Elk Island National Park occurred to Nahanni Butte (28 bison in 1980), Waterhen in Manitoba (34 bison in 1984), Hay-Zama in northern Alberta (29 bison in 1984), and Nisling River in the Yukon (34 bison in 1986). As some of the herds increase, the expectation is of the existence of several additional systems in which wolves and bison interact. Future research in those areas can be set up to investigate the role of wolf predation under different environmental conditions.

(iv) Proposal to Re-establish wood bison (1968) in Wood Buffalo National Park

After the Nyarling bison had been removed from the Park, renewed interest was generated in establishing them as a "pure subspecies" in Wood Buffalo National Park. Coupled with these plans was the objective of eliminating the diseases that had occupied so much attention during management programs in the mid 1960s. A plan was proposed in 1968, at the end of the management era, which called for a 20-year program that originally incorporated the following objectives:

1. Bring all major groups of bison inside and outside of the Park under control with fencing;
2. Eliminate all free-ranging bison once the above was accomplished;
3. Systematically test and cull fenced groups to produce a disease-free stock and environment;
4. Concurrently encourage an increase in the number of captive wood bison;
5. As soon as sufficient stock was available, and as soon as there were fenced buffer areas to guarantee that plains and hybrid animals could not intermingle with them, reintroduce both free-ranging and fenced groups of wood bison into Wood Buffalo National Park; and
6. As the wood bison increased, systematically eliminate the plains and hybrid stock until none remained in the north.

Because of the costs and logistics involved, and because of expected public opposition, this ambitious and idealistic plan was not approved. Mitchell (1976) lists the specific reasons:

1. Cost — in addition to the capital, operations and maintenance costs for the enclosures, the Sweetgrass abattoir had fallen into disuse and would have to be renovated, i.e., massive expenditure with no certainty of success.
2. Bison have been a national asset because they represent the largest free-roaming herds in the world. This value would be lost if the animals were fenced and managed under unnatural conditions.
3. Impossibility (within reasonable expenditures) of locating and eliminating bison remaining outside the fenced enclosures.
4. Likely criticism locally, nationally, and internationally if a large slaughter occurred.
5. Resistance by Fort Smith and Fort Resolution residents to removal of animals from Northwest Territories where bison were hunted and provided a source of food.

During 1973, plans were initiated to develop a strategy to bring back wood bison. After years of dedicated efforts with several successful attempts and one

unsuccessful attempt (bison release in Jasper National Park), a Wood Bison Advisory Group was formed during 1985 to provide advice on the management of wood bison. This eventually evolved into the Wood Bison Recovery Team, which recommended in its 1987 status report that the status of wood bison be downgraded from "endangered" to "threatened". At about the same time, around 1986, an interjurisdictional steering committee comprising representatives from seven different departments established a Disease Task Force to examine the disease-related problems in northern bison herds. Their final deliberations identified nine options for the management of disease in bison, the following four of which were recommended for serious review:

1. Maintenance of the status quo — no change.
2. Fencing of Wood Buffalo National Park to contain the diseased bison and prevent the spread of the diseases beyond the Park's boundaries.
3. Elimination of all diseased bison and replacement with a disease-free herd.
4. A composite plan to confine the diseases to the Park by combining strategically placed fences and buffer zones with active elimination of bison.

At the request of the federal Minister of Agriculture, an Environmental Assessment Panel was selected by the Minister of the Department of Environment in 1989 to review the socio-economic, environmental, and health problems associated with the bison in Wood Buffalo National Park. The resulting FEARO report was completed in 1990 and recommended depopulation and herd replacement (see earlier comments in the introduction). One cornerstone of the depopulation and replacement program was to re-establish a wood bison population in the Park. The 1990 proposal was in some ways similar to the 1968 proposal.

4. *Decline Era (1969-1991) — Years Of Rapid Decline*

Populations tend to generally increase or decrease exponentially. During the decline era (1969-1991), the number of bison in Wood Buffalo National Park decreased substantially. Plotting the data on a log scale (Figure 9) resulted in a regression of $r^2 = 0.849$, $p < 0.01$. When the years of drastic decline (1974) and years of stable numbers (1975-1980) are deleted, and the data plotted, without this information the regression was even more highly significant, $r^2 = 0.959$, $p < 0.0001$.

Upon a closer analysis, it appears that the decline went through four phases (Figure 9). That is, the decrease was gradual between 1969 and 1971 and more pronounced between 1972 and 1974. A drastic drop in numbers occurred in 1974, when an estimated 3,000 bison drowned in floods. Numbers stabilized from 1976 to 1981, and then declined to 1991. The data for 1980 was omitted because it was a poor survey.

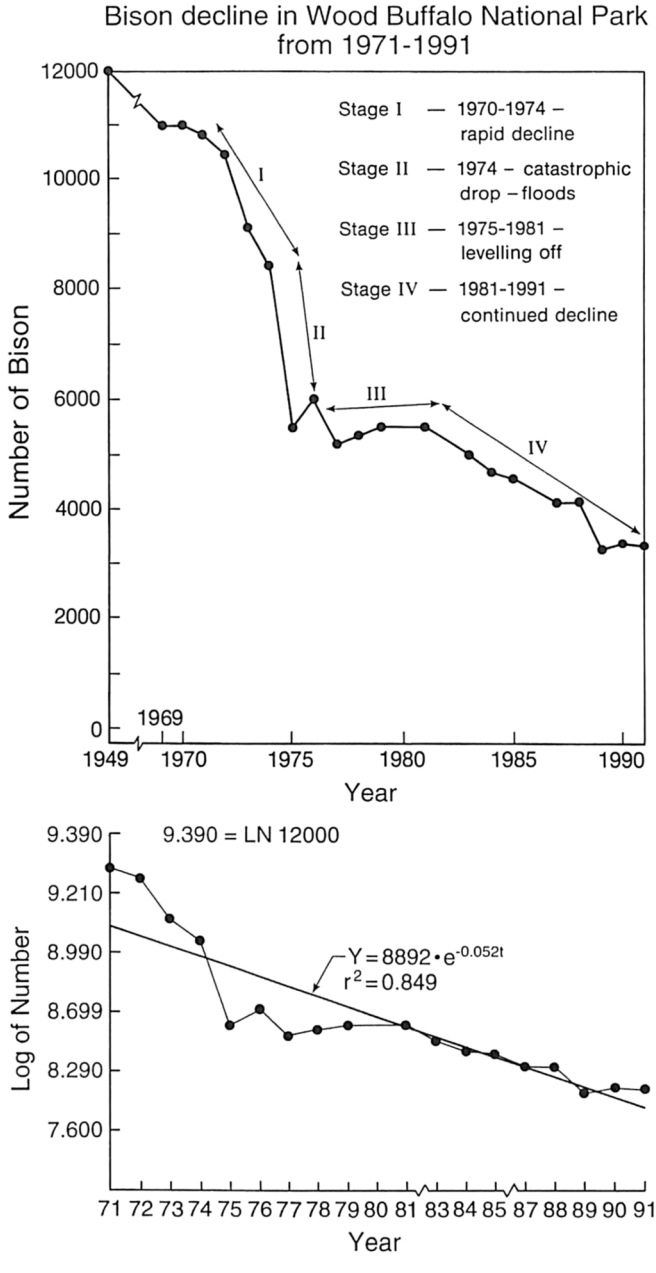


Figure 9. Bison population trends from 1970 to 1991 graphed to indicate two interpretations of the decline. In the top graph the decline is evaluated in a progression of four stages. A regression, based on a log scale suggests a monotonic downward progression where $r^2 = 0.849$, is shown in the lower graph.

Several other significant events characterized the decline era. First, the anthrax roundups that were begun during the mid 1960s were still in operation. Roundups likely had a significant impact on numbers due to stress related losses. Second, a long-term trend toward lower water levels and less frequent flooding in the Peace-Athabasca Delta was established. This trend began during 1969, after the completion of the Bennett Dam. The expected effect of these changes in the hydrological regime was a reduction in the amount and distribution of the primary foods of bison, *Carex* and *Calamagrostis*. Another aspect of this era was the phasing out of wolf control programs. The combination of less favourable conditions in the Delta, high roundup mortality, and high wolf predation may well account for the decline in the bison population during this period. We will examine these in turn under headings of physical factors, population parameters, disease, poaching, and wolves. Declines north and south of the Peace River differed in that most of the decline was in Area II (see Figure 28).

The Peace/Athabasca Delta, and associated areas in Wood Buffalo National Park, are of great importance to the northern bison populations. A review of the historical information available from the fur trade records, surveyors and explorers indicate that bison populations in the region were less common in the latter part of the eighteenth century and all of the nineteenth century than they have been in the twentieth century. Numbers increased in the area with the introduction of bison from Wainright in 1925 to 1928. Early population increases took place in the presence of introduced diseases but within limits of lower wolf populations and in with the occurence of periodic flooding of the Delta.

Large bison herds are present in spring and summer in the open delta areas south of the Sweetgrass Warden Station.

Deeply rutted extensive system of trails attest to the former abundance of bison in the Delta. The number of trails running along side a path have been reduced, evidence of the decreased use of some areas.

Three wood bison with different phenotypic expressions. These are descendants from 16 animals transferred from Needle Lake in the northwest corner of Wood Buffalo National Park to the Mackenzie Bison Sanctuary in 1963.

Calves are rust brown when they are young. This calf was born in late September. Peak calving period is in May.

Most calves observed in the field appeared to be healthy. This photograph was taken in early October, and on the same day as the calf above. Note milk saliva trail on the body of the cow.

III Physical Factors (1969-1981)

Among the physical factors one episode stands out above the rest. Major flooding of bison ranges took place in the Delta during the spring of 1974. As a result, the ice on previously flooded meadows and many creeks and rivers softened and cracked under the flood waters and many bison drowned after falling through (D. Donald; L. Flett pers. comm.). Water levels remained high throughout the summer and large areas of range were either destroyed by the water or were made inaccessible to bison. In some places the water level remained high well into autumn. During freeze-up these areas were again under ice and still more drownings resulted. The effects of wolf predation and other mortality factors magnified the impact on bison once numbers were sharply reduced. Drawdown of water during 1975 was sufficient to allow the bison to access the previously flooded meadows.

1. *Hydrological Regime of the Delta and its Importance to Bison Range*

A. *Introduction*

Approximately 31,000 years ago the Keewatin ice sheet of the Wisconsin glacier covered the Peace-Athabasca Delta area (Bayrock 1962). When the glacier retreated northward it left behind a huge basin. Part of this basin remained as Lake Athabasca, which was originally much larger than its current size. Most of the area that now forms the Delta was once part of Lake Athabasca. Because the ice finished retreating 10,500 years ago, the Delta has grown constantly (and the lake's size has decreased) through the deposition of new silt loads. This process still occurs whenever certain conditions cause the Delta's waterways to overflow. Temporary dams formed by ice at break-up cause the water to backup and eventually breach the levees of the Peace and Athabasca Rivers, resulting in flooding of meadows and recharging of perched lake basins and scouring of old Delta channels. High water in the Peace River, whether or not there is ice-jamming, also causes water to

flow into Lake Athabasca through the Riviere des Rouchers, Révillon Coupé and Chenal des Quatres Fourche that normally carry water out of the lake. Peace River water coming into Lake Athabasca forms, what has been referred to as a "hydrological" dam, which exacerbates flooding of the Athabasca River.

Variation in the Delta's hydrological regime has always been a part of the system — series of years with either above-average or below-average water levels have not been uncommon in the past (Bennet 1971). Water levels in the Delta are influenced by several environmental factors (e.g., trends in precipitation, rates of snow melt in the Peace River's catchment basin) that affect conditions in the Peace and Athabasca Rivers and the Delta itself. Bison are affected by the hydrological conditions in the Delta in a number of obvious ways; the two most important factors are drowning (see Management Era — Mortality Factors) and changes in the condition of bison ranges. Drowning may occur when bison fall through ice while crossing streams, lakes, and rivers, while changes in range conditions may result from prolonged flooding or prolonged drought conditions.

In the 1970s, approximately 75% of the bison in the Park used the Delta during some part of the year; all of the Park's bison depend on specific winter and summer ranges. The ratios changed in the mid to late 1980s. North of the Peace River, most of the important winter ranges are either directly associated with the Slave River and its tributaries (Murdock and Darough Creeks and the Hornaday River), or lie immediately west of the Slave River (Hay Camp Meadows). In the Delta, two main components — open delta areas and perched basins — are important as bison range. They support specifically adapted (delicately balanced) plant communities that are dependent on the surface and groundwater regimes. Optimum bison ranges occur on open delta land, primarily in the interval between contour elevations of 209.25 m and 209.85 m above sea level (Cordes 1975); significant flooding of those ranges occurs when the water level reaches 209.5 m. The land/water interfaces of perched basins are also important as bison range. Perched basins begin flooding at 209.85 m (Townsend, pers. comm.). By definition the perched basins are located at higher elevations than most of the Delta and are not connected to the main drainage system by surface channels, hence they are not recharged every year or even in every flood episode. In 1972, a flood at 209.85 m resulted in the recharging of some perched basins (Townsend, pers. comm.); approximately 78% of perched basins are refilled at 210.3 m (Peace-Athabasca Delta Project Group 1973). Major recharging of perched basins occurred during seven of the 20 years immediately prior to construction of the Bennett Dam. Six of the seven floods occurred during a cycle of high water years in the 1960s. Backswamps, which occupy higher (older) elevations in the Delta, are less frequently inundated by flood waters (Dirschl et al. 1974) and are less important as bison ranges than are perched basins and open delta lands, possibly because stagnation and incomplete plant decomposition render them nutritionally deficient.

Sedge (*Carex atherodes*) meadows and reed grass (*Calamagrostis canadensis*) communities are the most important sources of food for bison — up to 70% of the bison's annual diet and almost 100% of its winter diet is composed of these two species (Reynolds et al. 1978).

Throughout the year, bison in the northern areas exhibit an affinity for wet and mesic meadows containing sedges. It is the sedge meadows that are most frequently flooded; their maintenance actually requires periodic (preferably short-term) flooding. *Calamagrostis* communities occur on higher ground that floods less frequently. This type of vegetation (i.e., sedges and grass meadows), which is at the early end of the successional sequence, responds more rapidly to changes in the hydrological regime than does vegetation at the later end of the sequence (deciduous and coniferous forests). Initially, vegetation can be affected by seasonal or other short-term conditions. These effects can be offset by long-term trends, which are established by cycles of recurring events, and which ultimately have the greatest effect on bison ranges. Such trends can be of natural origin or the result of man's activities. For example, when sedges are covered by standing water caused by flooding, the result is poor vigour, low seed production (Cordes 1975), and the growth of long stems (up to 2 m) that are too weak to support the plant in air, and float on the water's surface (Cooper 1974). When high water levels persist, sedges lose their vigour and eventually die (Dirschl et al. 1974, Cordes 1975). If prolonged flooding has occurred, short-term drought conditions can have a positive effect on bison ranges by allowing areas that had been too wet to dry out. However, because sedges thrive best in specific moisture conditions, a prolonged drought would eventually result in the loss of sedge habitat. Because *Carex* and *Calamagrostis* can become established or eliminated within three or four years, either prolonged flooding or prolonged absence of floods can have disastrous effects on the total amount of bison range. Fortunately, the general diversity of levees, channels, ponds, and perched basins provides a range of opportunities, but they will provide fewer opportunities for bison food production if periodic floods are not restored.

Even when the distribution and amount of range is adequate, abnormally high water levels can restrict the accessibility of forage. Spring floods were a common occurrence on the open areas of the Delta; if water levels did not recede and stayed high through the summer, the forage covered during the spring would remain inaccessible to bison, and if the level has not fallen by freeze-up, this food will also be unavailable during winter. It has been shown for moose (Peterson 1977) and white-tailed deer (Verme 1969, 1977) that an adequate supply of food during the summer results in an increase in fat reserves in adults. This in turn increases their fecundity, and may also reduce mortality during winter when reduced food intake and increased exposure to cold can result in a weight loss sufficient to predispose an individual to disease and predation or kill it outright. Animals unable to accumulate fat reserves during summer would be at a distinct disadvantage; if their access to food was lower than usual during winter, their chance of survival would be further reduced. During 1962, a build-up of ice

occurred on some areas of the bison ranges (Park files 1963); because snow cover typically restricts access to food during winter, the further loss of access to range that was under ice could have been critical. Furthermore, the quantity of forage (biomass) available may have less effect on bison numbers than the nutritive quality of the forage. If the nutrient content of *Carex atherodes* and *Calamagrostis canadensis* [which may normally vary considerably during the annual life cycle, as has been shown in other species (Cook 1972)] is adversely affected when they are covered with water for long periods, the quality of this forage could be poorer than usual during winters that follow prolonged flooding. Calves born following winters in which food was in short supply and/or of lower quality may be less viable. Because a large proportion of bison ranges in the Delta are located in areas that are most easily and frequently flooded, any perturbation or anomaly in the hydrological regime of these regions could influence bison by reducing quantity and quality of forage.

As part of this study, conditions in the Delta between 1970/71 and 1980/81 were reviewed to determine whether the changes in bison numbers observed during this period were correlated with known hydrological events. This period was also compared with the period from 1947 to 1971. The long-term water-level data collected at Lake Athabasca between 1947 and 1980 were compared with the site-specific data from monitoring stations in the Delta (Cordes 1975, Cordes and Strong 1976; Cordes and Pearce 1977, 1978, 1979).

B. *Methods*

Historical fluctuations of the water level of Lake Athabasca, which were plotted from data in a summary by Townsend (1982a), were reviewed and summarized for three different periods: 1947-1967 (natural regime), 1968-1971 (construction and of Bennett Dam and subsequent filling of Williston Reservoir), and 1972-1981 (initial phases of Bennett Dam operation). The data for 1982-1991 (full operation of the Bennett Dam) was analyzed by consultants (Jaques 1990).

Between 1970/71 and 1980/81, the water level at Lake Claire (north bank of the Prairie River — Station 07KF002) was recorded daily by Alberta Environment. These site-specific data were obtained from the Inland Waters Directorate, Water Resources Branch, Ottawa. Each month of the study was divided into three eight-day periods and one period that contained the remaining days in the month. For each period, the daily water-level data was averaged, then plotted for the entire year. Critical flooding thresholds were recorded at 209.5 m (open delta flood zone) and 210.3 m (perched basin flood zone); when changes occur in the Delta, the critical flooding thresholds may change as well.

Freeze-up and break-up dates were recorded by the Water Surveys Division of Environment Canada at Fort Smith (Station 07KC001) and Fort Fitzgerald (Station 07NB001). The Water Surveys Division defined freeze-up and break-up dates as the times "when the presence of ice affects stage-discharge relationships." The freeze-up date is the first day on which there is a backwater effect caused by

ice, while the break-up date is the first day on which there is no backwater effect seen in the outflow channels. In the Delta's basins, freeze-up occurs earlier in fall and ice is retained longer in spring than in open channels.

The information used in this part of the study was stored and analyzed using the University of Alberta's Michigan terminal systems (MTS) system.

C. *Results And Discussion*

Information on trends of the water level of Lake Athabasca between 1947 and 1980, showing the generalized amplitude and duration of fluctuations in water levels, is illustrated in Figure 10. The years in which 70% or more of the perched basins probably flooded are marked by an asterisk. However, caution is required in drawing conclusions, because water levels in Lake Athabasca do not always reflect hydrological conditions in the Delta. More detailed information on water levels at Lake Claire between 1970/71 and 1980/81, showing the years during which drawdown on the Delta in the fall did not result in water levels lower than 209.5 m, is given in Figure 11. The actual dates of freeze-up and break-up of the Peace and Slave Rivers between 1953 and 1981 are shown in Table 4. G. Townsend (pers. comm.) utilized modelling information to determine the arbitrary freeze-up (October 17) and break-up (April 30) dates used to develop Figure 10.

The conditions at Lake Athabasca during the 33-year period from 1947 to 1980 were probably fairly typical of conditions in the past, because tree-ring growth during this period resembles that of the immediately previous 157-year period (Townsend 1972). On the basis of the available data, it was concluded that the 1950s were "dry" years; the 1960s [except 1968 and 1969 (both "dry")] were wet years, with eight years of flooding and two years of winter range freeze-up; and that the 1970s were generally intermediate, except for 1970, 1971, and 1975 ("dry") and 1974 ("very wet"). The 1950s resembled the 1970s, in that they were marked by three and four years of flooding respectively, and had no pronounced freeze-up of winter ranges.

Human activities have affected water levels at various times, beginning with the completion of the Bennett Dam (1968), which resulted in lower water flow in the Peace River (Dirschl et al. 1974) and the lower water levels in the Delta during the summers of 1968, 1969, and 1970 (Figure 10). Major floods of perched basins appeared to have occurred during seven of the 20 years prior to construction of the dam — one during the late 1940s, none during the 1950s, and six during the 1960s. There was no flooding of perched basins during the years in which the Bennett Dam was being filled (1968-1971). Icing of meadows, which takes place when the water levels in the Delta are high during the fall to early winter, occurred three times during the eight years immediately before the Bennett Dam was completed. Subsequently, a series of reviews of then pending problems precipitated the construction (and destruction) of several dams and weirs on the three outflow channels. The following is a summary of these events:

1971 — Quatre Fourches Dam built during October and November;
1972 — Quatre Fourches Dam raised during May;
— Quatre Fourches Dam partially washed out during June;
— Quatre Fourches Dam repaired during October;
1974 — Quatre Fourches Dam partially washed out during May;
1975 — Quatre Fourches Dam removed during December;
— Riviere des Rochers Weir built during June to October;
1976 — Révillon Coupe Weir built during January to March;
— Riviere des Rochers Weir completed.

Major flooding occurred once (1974) during the five years in which these dams and weirs were being constructed. The Quatre Fourches Dam prevented water from getting to the Delta by way of the Quatre Fourches River and Lake Athabasca (W.A. Fuller, pers. comm.).

Most of the important summer bison ranges in the Delta are not in the immediate vicinity of these weirs. The weirs did not have the desired effects in restoration of the Delta. Superficial evaluation indicates that they have not been effective in restoring and/or maintaining the hydrological regime to the natural condition that existed prior to construction of the Bennett Dam. Weirs tend to raise the minimum water levels without increasing the maximum levels which can only come from ice damming on the Peace River. The Peace-Athabasca Delta Implementation Committee (PADIC) 1987 study reviewed subsequent models and concluded that "The duration curve also shows that the peak Lake Athabasca levels are virtually restored...and that, lake levels above elevation 209.9 m are exceeded only 1-2% less frequently than under the natural regime". These data represent modeled results. Jaques (1990) used actual recorded water level values to determine that pre-Bennett Dam (1931-1967) peak summer flood levels on Lake Athabasca at Fort Chipewyan were 209.92 m, while post-Bennett Dam peak summer flood levels were 209.44 m (1976-1988). This study showed that levels above 209.9 m exceeded 30% less frequently under the weir regime than under the natural regime, not the 1-2% less frequency identified by the PADIC modelling study. Further study is required to identify and understand the magnitude of hydrologic impacts on the wetland ecosystems of the Peace-Athabasca Delta.

A closer review of the site-specific water-level data for the period from 1970/71 to 1980/81 reveals a cycle of dry-to-wet-to-intermediate conditions (Figure 11). The period from 1968 to 1971 was characterized by exceptionally dry years (Dirschl et al. 1974). Ice jams in the Peace and Athabasca Rivers caused flooding of open delta lands (and some flooding of perched basins) during late April (onset approximately 29 April) of 1972 (D. Donald, pers. comm.), which began a cycle of three years of high water levels (1972-1974). Information on the daily water-level conditions at Lake Claire during the spring of 1972 is shown in Table 5. This site-specific information is not available for the spring of 1974; drawdown was inadequate during the fall of 1973, so that when ice jams occurred during the spring of 1974, the water levels were already high and the monitoring station at Lake Claire was flooded. Water levels for 1974 were measured at Mamawi Lake, and because the Quatre Fourches Dam was still in place, the results are similar to those of Lake

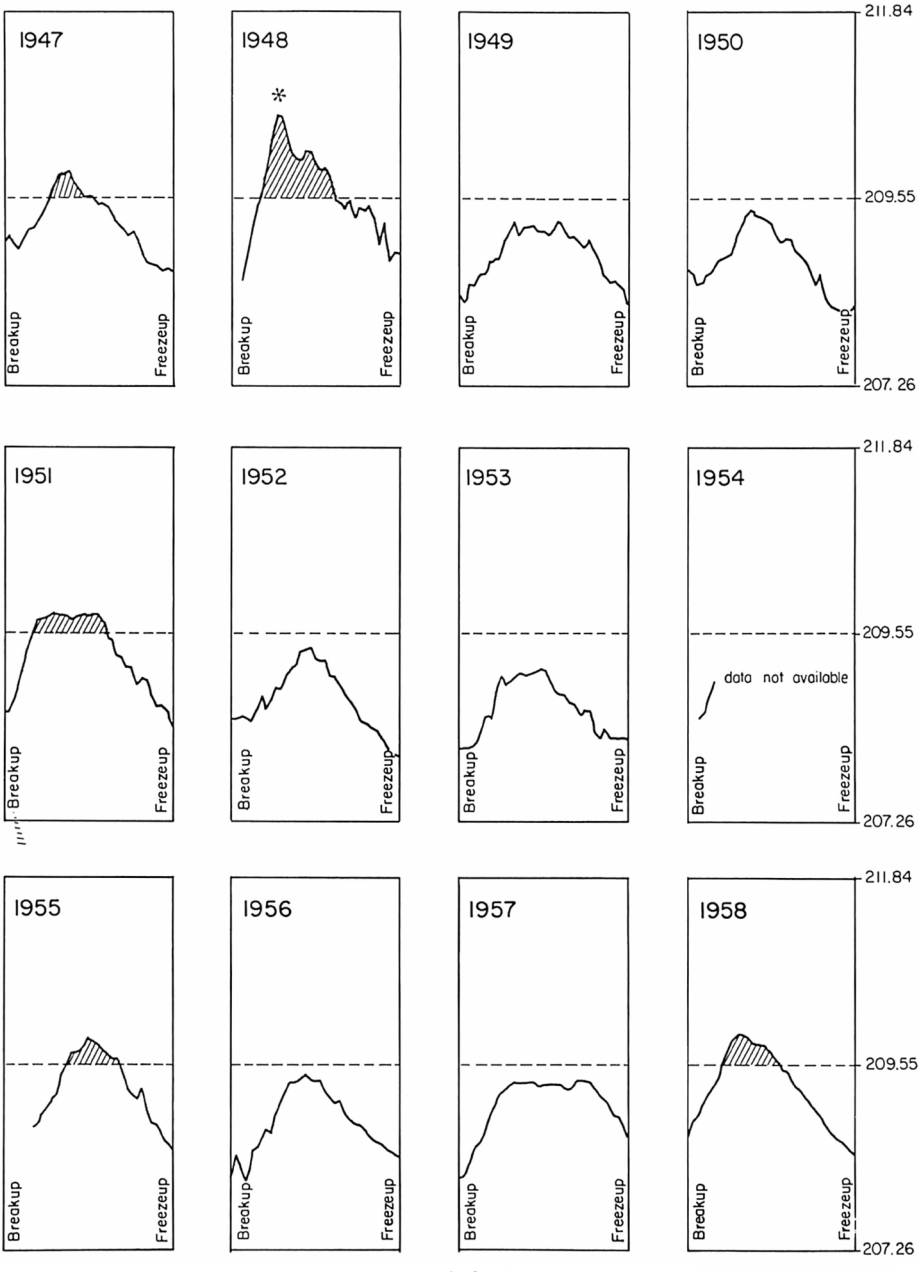


Figure 10. Summary of water-level trends for Lake Athabasca, 1947-1980 (Townsend 1982b). The bottom line of each graph represents 207.27 m asl, while the top line represents 211.84 m asl. The dashed line at 209.55 m indicates the level at which the major bison ranges in the Lake Claire and Lake Mamawi areas begin flooding.

* indicates flooding of 70% of perched basins.

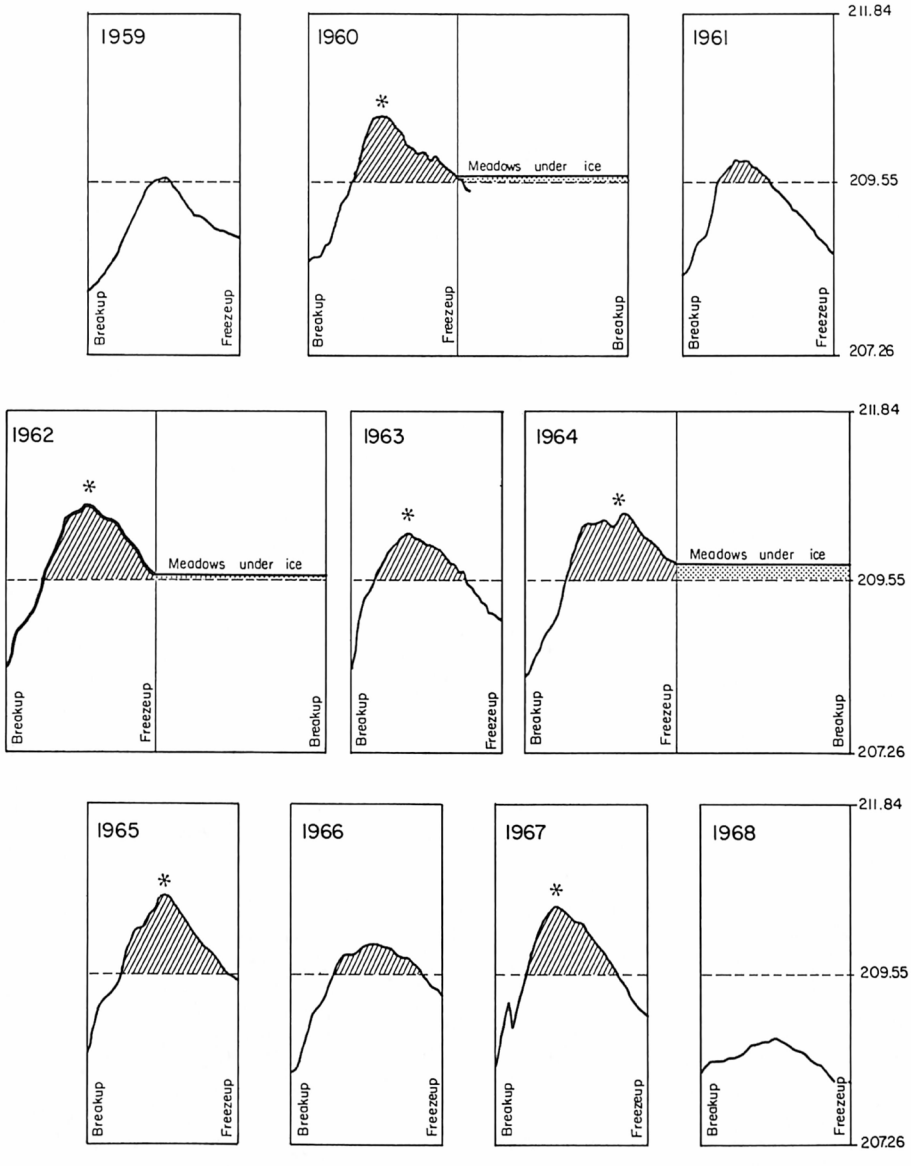
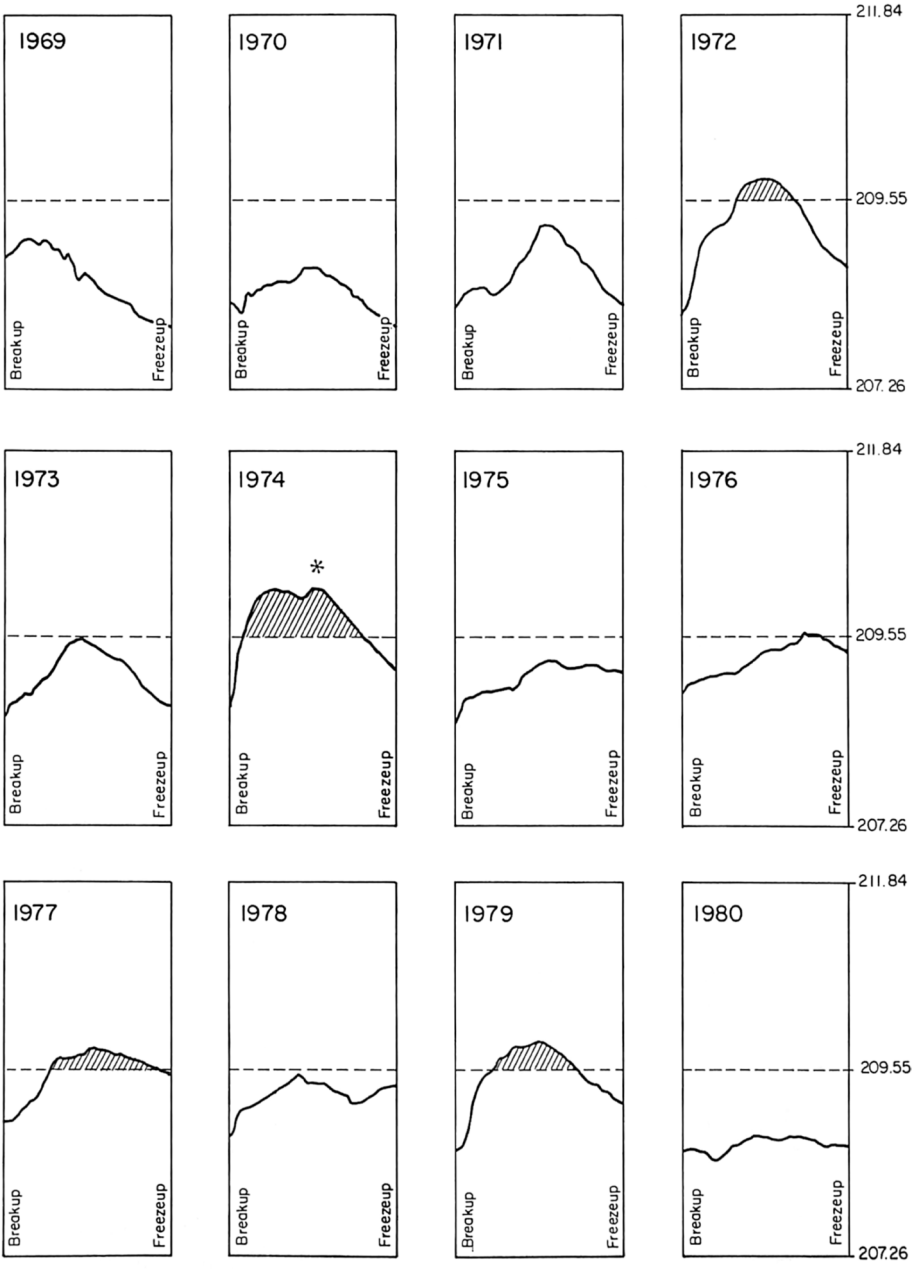


Figure 10. Continued.



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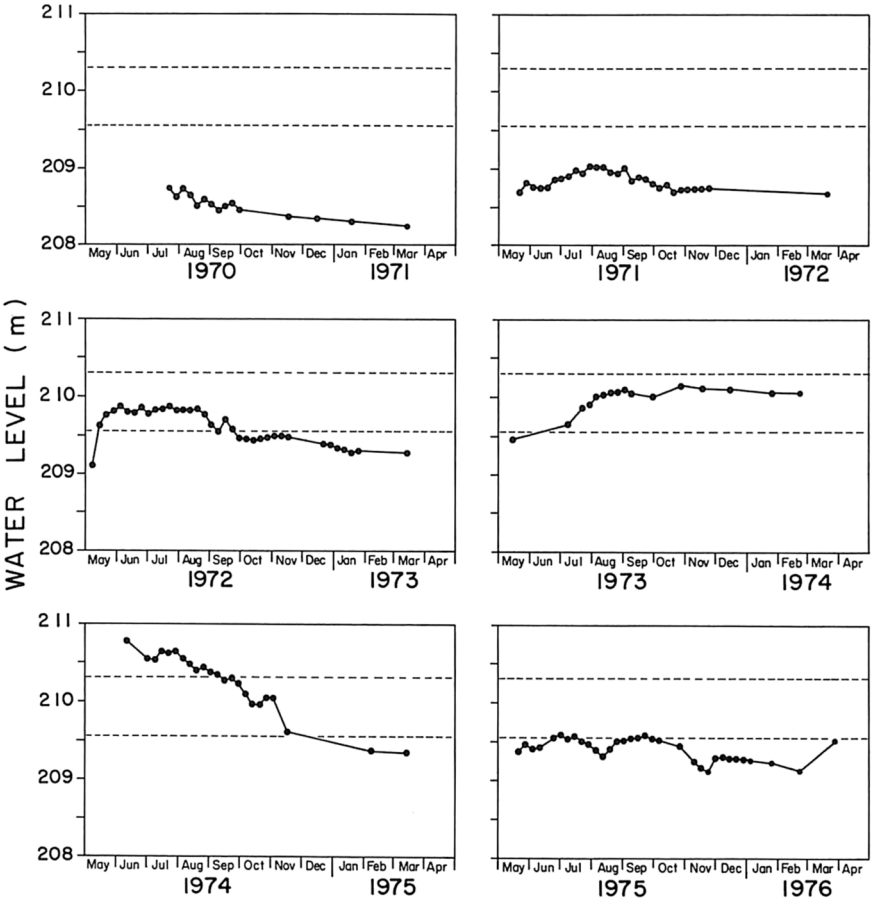


Figure 11. Fluctuations in water levels in the Peace-Athabasca Delta, as recorded at a monitoring station on the Prairie River, 1970-1981. Dashed lines represent critical flooding thresholds at 209.55 (open delta portion) and 210.3 m (perched basin flood zone; fromTownsend 1982b).

Claire. Fortunately, drawdown was relatively rapid the following spring because the Quatres Fourches Dam was partially washed out and created more stable conditions during the summer of 1975. Water levels were moderate during the summers of 1975 and 1976; they increased during the summer of 1977 and 1979, but were low during 1978 and 1980. Extremely high flooding of perched basins occurred only during the spring of 1974, although field evidence indicates that considerable recharging of perched basins also occurred during the spring of 1972 (G. Townsend, pers. comm.). Judging from the hydrological data, flooding of the *Carex* meadows associated with the open delta must have taken place during the summers of 1972, 1973, 1974, 1977, and 1979. Actual observations are summa-

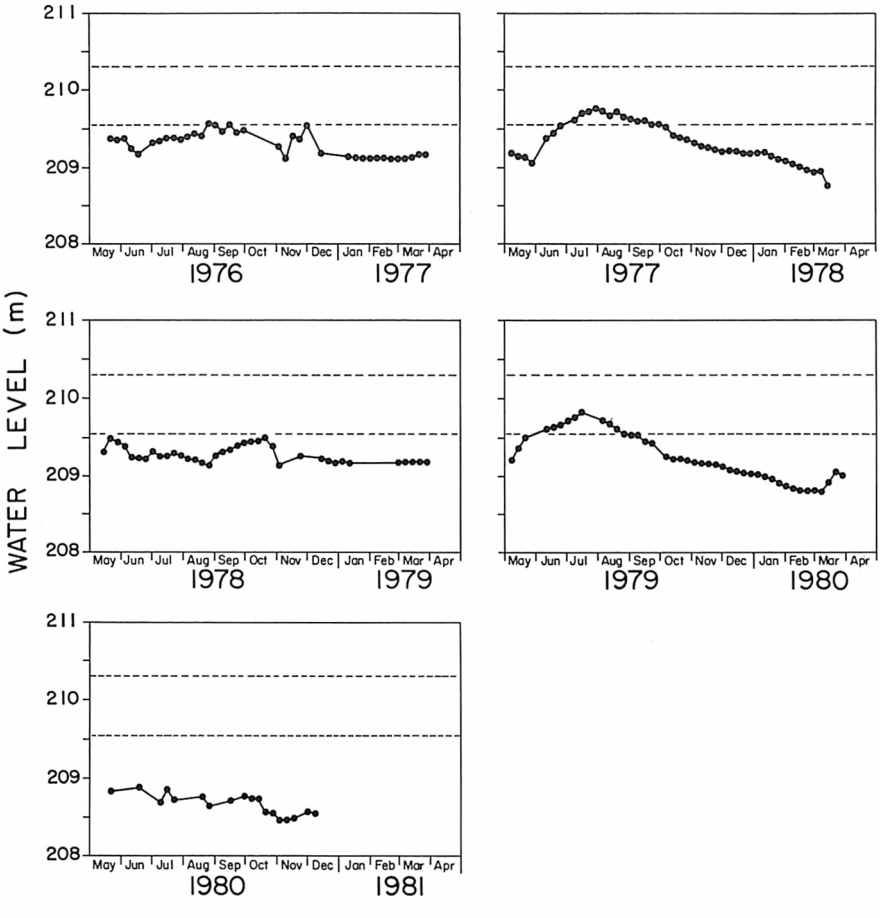


Figure 11. Continued.

rized in Table 6. Fall drawdown on the Delta was adequate during all years except 1973/74 and 1974/75, during which the icing of meadows apparently occurred. No information on field checks is available.

The data for break-up and freeze-up dates during any given year (Table 4) show no unusual deviations that suggest conditions that would lead to the drowning of bison. The freeze-up dates during 1963, 1970, 1974, and 1979 were somewhat later than average, whereas the break-up dates for 1976 and 1980 were somewhat earlier than average. The break-up date for 1974 was not unusual when compared with that for other years. The first drowning in that flood cycle was recorded during the fall of 1972 when bison crossed thin ice at Mamawi Lake (D. Donald, pers. comm.).

Table 4. List of break-up and freeze-up dates for the Peace River (Peace Point) and Slave River (Fort Fitzgerald), as recorded by the Water Surveys Division at Fort Smith, N.W.T. Data for 1955 and 1958 were not available.

	Break-up		Freeze-up	
Year	**Peace River**	**Slave River**	**Peace River**	**Slave River**
1953	-	8 May	-	23 October
1954	-	23 May	-	11 November
1956	-	11 May	-	25 October
1957	-	10 May	-	-
1959	-	20 May	5 November	16 October
1960	7 May	14 May	1 November	25 October
1961	5 May	19 May	3 November	1 November
1962	9 May	15 May	7 November	9 November
1963	-	11 May	15 November	17 November
1964	9 May	9 May	-	-
1965	-	-	9 November	10 November
1966	8 May	14 May	26 October	4 November
1967	14 May	17 May	6 November	6 November
1968	2 May	12 May	6 November	8 November
1969	24 April	5 May	26 October	8 November
1970	5 May	10 May	14 November	6 November
1971	29 April	5 May	30 October	1 November
1972	16 May	13 May	1 November	30 October
1973	4 May	7 May	5 November	5 November
1974	5 May	8 May	18 November	14 November
1975	4 May	8 May	31 October	4 November
1976	28 April	30 April	11 November	10 November
1977	26 April	3 May	7 November	9 November
1978	4 May	14 May	10 November	10 November
1979	14 May	20 May	13 November	14 November
1980	24 April	26 April	10 November	11 November
1981	7 May	11 May	15 November	29 October

After the drought between 1968 and 1971, most of the important *Carex* meadows were located between 209.25 m and 209.85 m asl (Cordes 1975). Cordes also observed that the succession of three "dry" years followed by three "wet" years favourably affected (with respect to bison range) about 30% of the vegetation cover on the transects sampled (Table 6). Presumably this represents a good sample of overall conditions in the Delta. Forty percent of the change affected vegetation that had become established during the three dry years prior to 1971 (or about 12% of the total vegetation on the transects), while 60% of the change affected vegetation that was present before the low-water years (or about 18% of the total vegetation on the transects) (Cordes 1975). We believe that the research by Cordes was significant in promoting a better understanding of the effects of hydrological changes on bison range.

Table 5. Water level conditions, as recorded at the mouth of Prairie Creek (Lake Claire), during the ice jam in the spring of 1972. The gauges at this location were flooded during 1974, so measurements for that year were made at Mamawi Lake Channel (at old dog camp).

	1972	1974
	Prairie River	**Mamawi Lake**
25 April	-	210.21 m
26 April	-	210.25 m
27 April	-	210.30 m
28 April	-	210.48 m
29 April	-	210.70 m
30 April	-	210.74 m
1 May	-	211.07 m
2 May	209.09 m	211.34 m
3 May	209.09 m	211.37 m
4 May	209.03 m	211.28 m
5 May	209.94 m	211.20 m
6 May	209.03 m	211.20 m
7 May	209.13 m	211.19 m
8 May	209.48 m	211.19 m
9 May	209.58 m	211.18 m
10 May	209.59 m	211.17 m

Source: Alberta Environment records.

Table 6. Summary of water levels, vegetation responses, and trends in the bison population in the Peace-Athabasca Delta, 1970-1981.

Year	Water levels	Vegetation Responses	Bison population trends
1970	Declining - all large lakes in the delta decreased by 28% in size (Dirschl 1972). Perched basins drying up.	Colonization of mud flats. In 1968, newly exposed areas (immature fen) slowing invasion by scattered seedlings of emergent aquatics, sedges, and grasses. Herbaceous plants present in 1969; by 1970, areas were covered by dense sedge meadows that existed prior to 1968 were evolving towards *Calamagrostis canadensis* meadows, reflecting drier conditions.	Calf counts high. Bison population high.
1971	Low; slight increase over previous three years because of ice jam on the Athabasca River. Rockfill weir constructed on Quatre Fourches in the fall.	Maturation of communities that changed as a result of drought years.	Bison population high.
1972	Spring flooding caused by ice jams in the delta; filling of perched basins. First year since 1968 with high water levels.	Not studied in detail, but changes occurred that led to the detailed studies of vegetation conducted during 1974.	Bison numbers declining.
1973	Water levels in the spring and summer were high; continued high levels during fall and winter resulted in icing of meadows. High fall and winter levels were attributed to the presence of the Quatre Fourches Weir.	Not studied in detail, but changes occurred that led to the detailed studies of vegetation conducted during 1974.	Bison numbers declining.

Table 6. Continued.

Year	Water levels	Vegetation Responses	Bison population trends
1974	Water levels during the winter of 1973/74 were high because of Quatre Fourches Weir. Ice jam during April and rapid rise of water to 211.36 m - these conditions were apparently exceeded only twice in the last 44 years (Cordes 1975). It is unlikely that the weir was responsible for extensive floods; however, because of the weir, peak flood levels may have been reached more quickly. Water levels threatened to stay high during the fall and winter, but wind and water levels caused a partial washout of the weir on 3 October 1974.	Since 1971, flooding has resulted in observable changes in the vegetation base. Transect studies show *Carex*-dominated meadows reduced by 53% in acreage (Cordes 1975). *Scolochloa festucacea* presence has increased in sedge meadows *Carex* was in reduced vigour where it did persist. Prolonged flooding reduced *Calamagrostis* meadows to 65% of that prior to 1968.	Declining; because of rapid rise in water, bison were trapped in the delta and from 1000-2000 (possibly more) perished.
1975	Removal of Quatre Fourches Weir; subsequently water levels dropped considerably. Bare mud flats with immature fen have increased noticeably over 1974 levels. Flood conditions in both 1975 and 1976 were below the long-term mean maximum. Riviere des Rochers Weir constructed.	*Calamagrostis* and *Carex* meadows increased by 223% and 52% respectively and there was a 45% reduction in *Scolochloa*. Noticeable increases in vigour of sedges and reed grass. Cordes and Strong (1976) established a new transect through bison range (Sweetgrass area). These meadows are located at maximum elevation for semi-active delta land and probably survived the 1972-1974 floods.	Slight increase in bison since surveys during the winter of 1974.

Table 6. Continued.

Year	Water levels	Vegetation Responses	Bison population trends
1976	Riviere des Rochers Weir was completed, but there was little change in the water levels between 1975 and 1976 (Fig. 10). Falling water levels causing potential problems in relation to re-charging of perched basins. It appears that the weir's presence has resulted in increased minimum levels, rather than increased maximum levels (Cordes and Pearce 1977).	Vegetation showed little change; slight increases in immature stages of *Carex* and *Calamagrostis* as *Scolochloa* continued to decrease.	Slight decrease in bison since surveys during the winter of 1975.
1977	Conditions similar to those during 1975 and 1976, but early-spring to late-summer levels were slightly higher (Fig. 10). Flood peaks necessary to recharge perched basins were not attained. Water level amplitudes during the growing season were lower than long-term "Normal" conditions (Cordes and Pearce 1978).	Vegetation is under water longer than before (water over 209.7 m was maintained for 3 instead of 2 months and above 209.1 m for 7 1/2 instead of 4 months. This affected species diversity and plant vigour. Increase in areas of immature vegetation.	Bison were excluded from some summer range, greater concentration on higher, drier meadows resulting in plant destruction, soil exposure, and invasion of fox tail (*Hordeum jubatum*) and sow thistle (*Sonchus arvense*) (Cordes and Pearce 1978).
1978	Water levels dropping compared with 1977 conditions (Fig. 10), although levels were higher than "normal" during the fall and winter. Low perched basins re-charged.	*Calamagrostis* has been taking over some *Carex* communities. Continued drying of the delta and stabilization of water regime contributed to a deterioration of both communities (Cordes and Pearce 1979). Weir construction has kept low water levels higher than desirable.	Bison numbers are stable from previous year's surveys.
1979-1981	Drying trend continues.		Bison numbers; stable to declining.

Although predictions are always speculative, some thoughts on the effects that long-term flooding of the Delta could have on bison are in order. The importance of the Delta as both summer and winter range for the total bison population is obvious; during winters in the 1980s, up to 75% of all bison in the Park were found in the Delta region. This is a good indication of the productivity of the area. Estimates of the total area occupied by each type of habitat in the Peace-Athabasca Delta were calculated for 1970 (Peace-Athabasca Delta Project Group 1973). Of a total of 1,533,000 ha (including open water, mud flats, and areas of emergent vegetation), approximately 367,000 ha, or 24% of the area, was probably important as bison habitat. Another study (Jaques 1990) concluded that the productive vegetation communities have decreased throughout the entire Delta from 126,500 ha in 1976 to 97,900 ha in 1989. While this amounts to a reduction of productive wetlands of 23%, this loss actually represents a 47% reduction in that area of the Delta where wetland habitat is important. Furthermore, recent studies (Jaques 1992) indicated that productive perched basin portions of the Delta have lost 33-65% of the productive vegetation communities from 1976-1989. Modelling of satellite images has indicated that unless hydrologic conditions change, almost two-thirds of the potentially productive wetland habitat will be lost by the year 2035.

A short-term change in water level is not a crisis; however, prolonged retention of water at flood levels, or at the other end of the spectrum, a prolonged drought, is critical. Because the majority of important winter ranges north of the Peace River are located in mesic and wet areas they are presumably affected by long-term changes in that area's hydrological regime in a manner similar to that which is seen on the Delta; details of the relationship between water levels and bison range north of the Peace River have not been studied.

The availability (supply and accessibility) of forage is only one component of any discussion of the Delta's carrying capacity (potential population) versus its actual population. Some bison live on the Delta year-round, while others occupy its ranges only during the winter. The relationship between carrying capacity and the number of bison present at any given time of the year is not clear. In the 1990s there are approximately 1/3 to 1/2 fewer bison on the Delta than there were during the 1960s and early 1970s. On the basis of survey data from 1971, Townsend (1972) developed a computer model that projected a carrying capacity of 30,000 bison for the Delta area. Novakowski (Park files) calculated that if the carrying capacity was one bison per 30 acres, the whole Park could maintain 81,066 bison. There is no firm evidence to support or refute these figures, but given the size and productivity of the meadows, it is not unreasonable to suggest that the Park could support more than the 3,000 plus bison that are currently there. Reynolds et al. (1978) reached a similar conclusion (i.e., that the population is below carrying capacity) for the herds in the Slave River Lowlands.

The elevation in different parts of the Delta varies little. Because *Carex* has specific soil and moisture requirements, it is unlikely that it would rapidly displace other communities at higher elevations if long-term flooding of the Delta eliminated its habitat at lower elevations, because the soil's composition and formation at

higher elevations would be different. This would produce an unsuitable moisture regime. On the basis of this review, it appears that, for bison, the ideal hydrological regime in the Delta would include high spring water levels that regularly exceed 209.5 m and periodically (about once every three years) exceed 210.3 m. In all years, drawdown to approximately 209.25 m is important. This regime would preserve both *Carex* and *Calamagrostis* communities. If the current trend toward drying out of the Delta does not reverse, the consequences to the bison population could be critical in the long run.

2. *Winter Severity*

A. *Introduction*

Weather conditions during winter influence the survival, productivity, and distribution of bison in boreal environments (Fuller 1960, 1966; Meagher 1971, 1973; Van Camp 1975). According to Fuller (1966), "winter is undoubtedly the most stressful season for bison." Deep snow, snow crust, low temperatures, severe wind chills, and prolonged periods of snow cover during the spring are also stressful as they influence the condition of the cows when they are about to give birth. Similarly, an ungulate's ability to cope with winter is influenced by its condition going into that period. Factors that may influence condition include insects, disease, and the availability of forage during the previous spring, summer, and autumn. How early the first substantial snow fall occurs in the fall is also important. Deep snow may be stressful and thus may affect the survival of calves (Van Camp 1975), old, and weak adults. The amount and duration of snow cover influences the availability of forage during the winter (and thus the distribution of bison on winter ranges). It is known for elk (*Cervus canadensis*) that the condition of the developing fetus is partially determined by how well cows overwinter (Thorne et al. 1976). Whether the demands of fetal growth exceed maternal metabolic needs in bison is not known. In moose, weight gains of calves were highest in years with mild winters and average net gains from fall to winter were lowest in years of greater snow depths (Cederlund et al. 1991). Because moose are browsers and bison largely grazers, one would expect the effects would be even greater on bison.

Historical records (Dawson 1881, Whitney 1896, Preble 1908, Raup 1933, Soper 1941, Roe 1981) suggest that in some years midwinter thaws followed by freezing can limit the availability of food. These conditions occurred, with apparently devastating consequences, in the latter part of the 19th century. Raup (1933) also reported that a period of freeze-thaw conditions occurred during 1927/28. Although such conditions were not recorded in Wood Buffalo National Park during the decline period (1970/71 to 1990/91), a snowstorm in the adjacent Slave River lowlands during the autumn of 1974 that was followed by melting, refreezing, and freezing rain (sleet) might have led to the deaths of bison found during March of 1975 (Calef 1975). The high water levels that resulted from the spring flood during 1974 and the sheets

of ice that formed on much of the Delta's range during the following fall and winter created similar conditions (i.e., restricted accessibility and distribution of food).

The winters between 1970/71 and 1980/81 varied in severity, so it is possible that bison population dynamics were differentially affected from year to year. Because precise measurements of past conditions could not be obtained, cause-and-effect relationships cannot be identified with certainty. Although an overview of the relationship between the causes and consequences of annual variation in the severity of winter can only touch on trends and on any major events that differ from the norm, it is nevertheless worthwhile to examine the relationship between the severity of winter weather and observed changes in bison numbers during the decade of steep decline (1971 to 1981).

B. *Snow Conditions*

i) Introduction

Snow can increase the mortality and decrease the fecundity of ungulate populations by restricting their movements (Telfer and Kelsall 1979) and by reducing the availability of food (Van Camp 1975, Mautz 1978). Furthermore, some age and sex classes may be differentially stressed by the debilitating effects of snow, as is seen in elk. Bull elk generally deplete their fat stores during the rut and thus enter winter with low reserves (Flook 1970). This could also be true of bison, but since their rut is earlier, they may regain some of their fat before the onset of winter. C. Gates (pers. comm.) believes that bulls in the Mackenzie Bison Sanctuary recover after the rut and are in better physical condition in spring than in the fall. Smaller animals with low fat reserves, including calves, are at a disadvantage and may be disproportionately affected by deep snow. Although Soper (1941) did not consider snow depth to be a factor that contributed to calf mortality, Van Camp (1975) showed that snow that exceeds a critical depth of 50-60 cm can contribute to the mortality of bison calves. Adults are impeded by depths greater than 65-75 cm (Van Camp 1975). In this report, 55 and 65 cm were used as the critical limits for calves and cows respectively; 40 cm was considered the depth at which bison are first stressed by snow, depending on other physical parameters. The critical depth is probably slightly higher for mature bulls, which are on the average, approximately 18% taller than mature cows (180 cm at the shoulder versus 152 cm) (Banfield 1974). The scale drawings of a bison calf in its first winter and an adult bull (Figure 12) provide a rough means of comparing the potential effect of any given snow depth on the mobility of bison of different sizes. Deep, soft snow forces animals to abandon a normal gait and switch to a more energy-expensive method such as bounding. Problems related to movement through deep snow are partially overcome by the formation of trails and movement in single file.

Because bison are predominantly grazers, and must reach forage under snow, deep snow makes foraging more difficult. Snow depth affects forage availability less in sedge meadows than in upland meadows because the structure and biomass

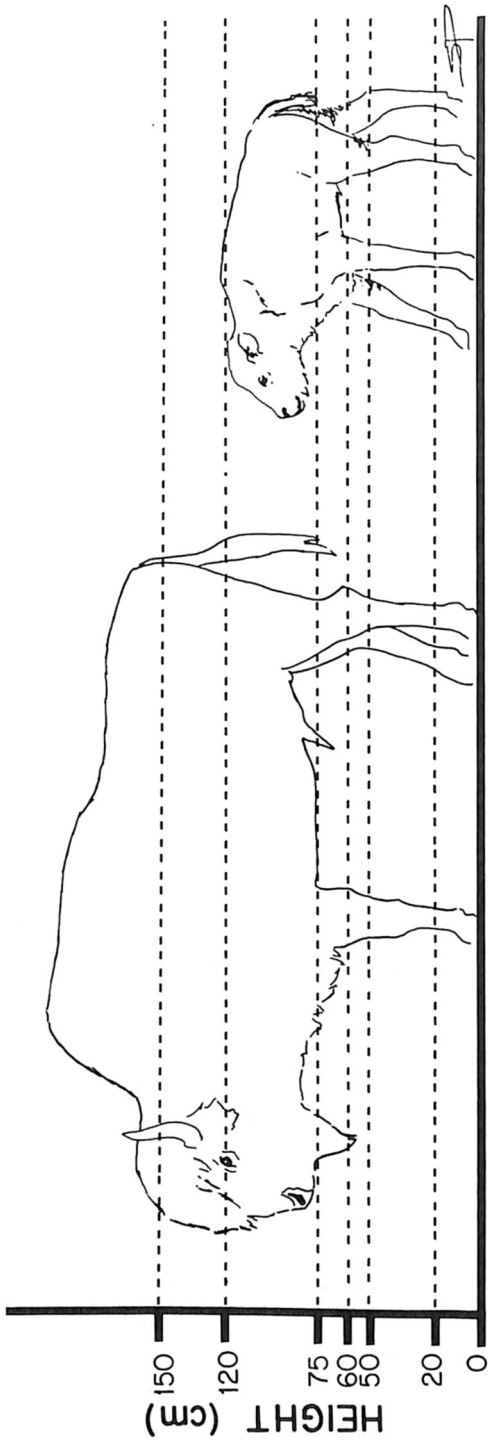


Figure 12. The approximate height (cm) of the various body parts of a mature bison bull and of a bison calf during its first winter (adapted from Van Camp 1975).

of vegetation in wet meadows allows snow to fall through the tall culms and form a less compact cover than for snow falling on shorter grass in upland situations.

Bison use three movements of their massive heads — swinging, nose pushing, and chin pulling — to sweep away snow to form feeding craters. Pawing, which is used by most North American ungulates, is seldom used by bison. The feeding craters of individual bison coalesce and form group craters. Because of snow metamorphosis, once an area has been disturbed the vegetation is locked into a crust and is essentially inaccessible until the snow melts.

Snow specific gravity (the weight of a given volume of snow/the weight of an identical volume of water) is a less obvious characteristic that affects the ability of ungulates to cope with winter. Movement and feeding are less difficult in soft, powdery snow than in dense, heavy snow. Because the density of snow tends to increase as winter progresses, the amount of work required to move snow and open up feeding craters also increases. One of the best studies on the subject was conducted by Van Camp (1975), who estimated that in Elk Island National Park, the amount of work required to move a given volume of snow doubles between mid January and mid March. One could expect that head swinging would increase to overcome the added resistance that results when snow becomes more dense. Observations show that this is not the case, suggesting that bison obtain progressively less food as the density of snow increases. Van Camp (1975) observed that calves abandoned head swinging when snow density reached 0.18 to 0.20 and snow depths exceeded 60 cm. Adult and subadult bison decreased head swinging at the same densities, but increased the use of other methods; nonetheless, head swinging remained the most frequently used means of clearing snow. For the purposes of this report, densities exceeding 0.20 are considered critical.

Snow hardness, which measures the resistance of snow cover to force applied to it, also affects the behaviour of ungulates. At high hardness values there is a positive correlation between hardness and density (Benson 1962), although the relationship is not consistent. Hardness probably has less overall impact on bison than does snow depth and density, except after winter freeze-thaw sequences, as discussed earlier.

When snow depths exceed 65 cm and densities exceed 0.20 for long periods, one could predict that fewer than the maximum potential number of calves would be born during the following spring, and that the calves that were born would be less robust (lower viability) and have a lower rate of survival during the subsequent summer than those born following milder winters (because the former were *in utero* during a more energetically-stressful period). Thus the calf/cow ratio during summer should be lower following winters with deep snow than it would be after winters with shallow snow. Similarly, calves born after a severe winter may have a lower rate of survival during their first winter (especially if this winter has high snow densities and prolonged periods with snow cover greater than 55 cm) than calves born after a mild winter. This effect could possibly be detected in yearling counts made during the following spring. Thus the most immediate impact (i.e., from one year to the next) of a winter with severe snow conditions would be on calf survival. When the cohorts that would be most affected (i.e., calves born immediately after a severe winter) approach reproductive maturity

2-3 years later, they may be smaller and experience delayed reproductive maturity. Therefore, the greatest impact of a severe winter may be delayed. Thus the severity of snow conditions may influence the reproductive dynamics of the bison population directly, by reducing the rate of calf survival, or indirectly, through either immediate or delayed reductions in the rate of calf production.

Results from some of the studies on calf production and winter severity in the Bison Sanctuary (1986-1989) do not show any relationship between snow conditions and calf production (C. Gates, pers. comm.). Mech et al. (1987) evaluated cumulative influences of snow on nutritional status of female white-tailed deer and concluded effects were transferred to several generations.

ii) Methods

Snow density data for the Fort Smith (1970-1979) and Fort Chipewyan (1975-1979) airports were obtained from the Atmospheric Environment Service (AES) of Environment Canada and from Alberta Environment respectively. Snow depths (recorded at mid month and month-end) for Fort Smith and Fort Chipewyan between October and March, 1965/66 to 1980/81, were also provided by AES. For the purposes of this report, the snow conditions at Fort Smith were considered to be representative of northern park conditions (Area I), while snow conditions at Fort Chipewyan were considered to be representative of more southerly conditions (Area II). Because the Park covers a large area, one would expect that local conditions often differ from the average conditions at these locations.

The first criterion used to determine the severity of winter snow conditions was the duration of the period of critical snow depth (DPCSD — number of months in which snow depths exceeded 55 cm for calves, 65 cm for adults). The duration of the period of critical snow depth is referred to in the text as DPCSD. The duration of this period was calculated by determining the distance between the points (measured in days) at which the snow depth curve intersects with the critical snow depth line, and dividing this distance by the number of days in the month. The durations of the periods of critical snow depth at Fort Smith and Fort Chipewyan were calculated separately to determine if differences existed between them.

The area of the snow depth curve that is above the critical value (55 cm) was used as a second index of the severity of winter weather. This was measured using a Cordi planimeter. Using this method, the measurement of the duration of the period of critical snow depth is combined with the measurement of the extent to which the snow's depth exceeds the critical level. These values are expressed as a percentage of the largest area (which indicates the most severe conditions) recorded at each station. For reasons discussed in a subsequent section, the final ranking was made on the basis of the duration of the period of critical snow depth (55 cm) for the Fort Chipewyan area.

When the data was reviewed, more emphasis was placed on the importance of snow depth, but snow density was also considered. Data on snow hardness were not available. The severity of snow conditions during the years of sharply declining numbers (1970/71 to 1975/76) and the years of stable or more slowly declining

numbers (1976/77 to 1980/81) were examined separately for Area I and Area II. Both periods were also compared with the five-year period between 1965/66 and 1969/70 to determine whether the decline observed between 1970 and 1975 was precipitated by the conditions of one or more winters before the decline began.

Using the duration of the period of critical snow depth, the severity of winter snow conditions during the period of sharply declining numbers (1970/71 to 1975/76) was compared with the severity of the conditions during the period of stable or slowly declining numbers (Mann-Whitney U-test, 1-tailed). The Kruskall-Wallis test was used to compare the mean annual snow depths for 1965-1970, 1971-1975, and 1976-1981 with long-term mean snow-depth conditions at Fort Smith and Fort Chipewyan. Mean annual snow depths at Fort Smith and Fort Chipewyan were compared to determine whether the snow depths in the winter ranges north and south of the Peace River were similar. It was assumed that data from these two sites generally reflected the trends in snow depth for the primary range in the Delta and in the Hay Camp area. For both locations, a Spearman's rank correlation was used to examine the relationship between the severity of snow conditions determined from the DPCSD and the severity determined from the snow depth values. A Wilcoxon paired-sample test was used to compare the duration of the periods of critical snow depths at Fort Smith with those at Fort Chipewyan. Differences were considered to be statistically significant at $p < 0.05$.

iii) Results and Discussion

The results of snow density measurements taken at Fort Smith (1 December 1970 - 1 May 1979) and Fort Chipewyan (23 January 1975 - 27 March 1979) are summarized in Tables 7 and 8. Densities greater than 0.20 were usually recorded only during April. Similar densities were reached earlier (at the end of February) in Elk Island National Park during 1973/74 (Van Camp 1975). If generalizations can be made from only one year's data, it may be that the snow in Wood Buffalo National Park is less dense, on the average, than the snow in Elk Island National Park. Consequently, at equal snow depths, the bison in Wood Buffalo National Park may generally be less impaired by snow than the bison in Elk Island National Park. The critical snow depth values used in this report (55 cm and 65 cm) were originally calculated for Elk Island National Park (Van Camp 1975). If the average snow density in Wood Buffalo National Park is lower than that in Elk Island National Park, it is possible that the critical snow depths in Wood Buffalo National Park are actually higher than the values that have been used, and that the frequency of critical snow conditions in Wood Buffalo National Park is inflated in our calculations. However, detailed observations of bison behaviour in snow of various densities would be necessary before critical values could be adjusted. In any case, the comparison of snow depth data is a reasonable method of evaluating the relative severity of snow conditions within and between years.

The mid month and end-of-the-month snow depths recorded at Fort Smith and Fort Chipewyan for the winters between 1965/66 and 1980/81 are plotted in Figures 13-16. The snow depth information for each winter is summarized in Table 9;

Table 7. Snow density values for Fort Smith, N.W.T., 1970/71 to 1978/79 (calculated from data provided by AES, Environment Canada). — indicates no snow. x indicates no data collected on that date.

	1970/71	**1971/72**	**1972/73**	**1973/74**	**1974/75**	**1975/76**	**1976/77**	**1977/78**	**1978/79**
Nov. 1	x	0.077	x	x	x	—	0.079	x	x
15	x	0.121	x	x	x	0.215	0.174	0.100	0.113
16	x	x	x	0.050	x	x	x	x	x
18	x	x	0.088	x	x	x	x	x	x
Dec. 1	0.125	0.117	x	x	x	0.212	0.139	0.094	0.108
3	x	x	0.115	0.112	0.102	x	x	x	x
15	0.143	0.170	0.122	x	x	0.211	0.136	0.091	x
18	x	x	x	0.070	x	x	x	x	x
20	x	x	x	x	0.073	x	x	x	x
Jan. 1	0.113	x	x	x	x	0.154	0.133	0.097	0.143
3	x	0.125	0.167	x	0.120	x	x	x	x
4	x	x	x	0.174	x	x	x	x	x
15	0.125	x	x	0.150	x	0.173	0.173	0.176	0.144
17	x	0.127	0.108	x	0.143	x	x	x	x
Feb. 1	0.147	0.124	x	x	x	0.191	0.158	0.142	0.189
2	x	x	0.148	x	x	x	x	x	x
3	x	x	x	0.201	0.131	x	x	x	x
15	0.152	x	0.135	x	0.186	0.208	0.151	0.121	0.130
18	x	0.149	x	0.092	x	x	x	x	x

Table 7. Continued.

	1970/71	1971/72	1972/73	1973/74	1974/75	1975/76	1976/77	1977/78	1978/79
Mar. 1	0.138	x	x	0.185	x	0.165	0.155	0.124	0.141
2	x	x	0.141	x	x	x	x	x	x
3	x	0.135	x	x	0.143	x	x	x	x
14	x	x	0.149	x	x	x	x	x	x
15	0.186	x	x	0.204	x	0.176	0.142	0.121	0.119
18	x	0.079	x	x	0.098	x	x	x	x
Apr. 1	0.207	x	x	x	x	0.205	0.200	0.105	0.541
3	x	x	x	x	0.163	x	x	x	x
4	x	0.159	0.202	0.199	x	x	x	x	x
10	x	x	x	0.277	x	x	x	x	x
14	x	x	0.254	x	x	x	x	x	x
15	0.207	x	x	x	x	0.141	0.333	—	0.187
16	x	x	x	x	0.244	x	x	x	x
17	x	0.235	x	x	x	x	x	x	x
May. 1	x	x	—	x	—	x	x	x	0.276

Table 8. Snow density values for Fort Chipewyan, Alberta, 1975/76 to 1978/79 (calculated from data provided by Alberta Environment). x indicates no data collected on that date.

	1975/76	1976/77	1977/78	1978/79
Dec				
22	x	0.172	x	x
Jan				
6	x	0.136	x	x
18	x	0.157	x	x
23	0.128	x	x	x
Feb				
10	x	0.106	x	x
17	0.163	x	x	x
29	x	x	0.193	x
Mar				
1	x	x	x	0.173
2	0.150	0.105	x	x
13	x	x	x	0.193
14	x	0.194	0.185	x
15	0.172	x	x	x
27	x	x	x	0.230
Apr				
1	x	0.200	x	x
2	x	x	0.229	x

long-term monthly averages are plotted in Figure 17. The mean annual snow depths at Fort Chipewyan were significantly higher than those at Fort Smith (paired t-test; $p < 0.04$), but as expected, there is a positive correlation between the mean annual snow depths at the two locations (Spearman's rank correlation; $p < 0.002$). The mean duration of the period of critical snow depth (Table 10) was significantly longer at Fort Chipewyan ($\overline{X} = 1.22$ months) than it was at Fort Smith ($\overline{X} = 0.37$ months; Wilcoxon paired-sample test, 1-tailed; $p < 0.01$). On the other hand, snow cover persisted later into spring at Fort Smith than at Fort Chipewyan (Figure 17).

Table 9. Mean snow depth (cm) for each winter (1 October - 31 May) at Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1965/66 to 1980/81 (calculated from data provided by Alberta Environment).

Year	Fort Chipewyan	Fort Smith
1965/66	24.63	25.69
1966/67	42.63	31.13
1967/68	34.14	31.29
1968/69	25.44	16.00
1969/70	19.13	19.69
1970/71	29.94	20.81
1971/72	38.88	32.00
1972/73	26.00	24.88
1973/74	43.31	29.81
1974/75	23.56	24.19
1975/76	36.69	31.88
1976/77	23.06	24.06
1977/78	27.13	19.44
1978/79	18.19	20.81
1979/80	13.86	22.60
1980/81	22.93	19.13

The mean duration of the periods of critical snow depth (>55 cm) recorded at Fort Chipewyan was significantly longer during the years in which bison numbers declined sharply (1970/71 to 1975/76) than during the years when the population was stable or declining more slowly (1976/77 to 1980/81) ($p < 0.05$). However, no such relationship was found for Fort Smith ($p > 0.10$). The latter findings were not unexpected, because the snow depths at Fort Smith rarely exceed 65 cm.

When snow depth values are used as an indicator, the results also show that winters were more severe during the years of sharply declining numbers (1970/71 to 1975/76) than during the years of stable or more slowly declining numbers (1976/77 to 1980/81). The difference between the two periods was statistically significant ($p < 0.05$). Comparison of the means of the duration of the periods of critical snow depth (Table 10) for the years of sharply declining numbers and the years of stable or slowly declining numbers with the long-term average (Figure 16) also supports the conclusion that winters between 1970/71 and 1975/76 were more severe than the long-term average (Table 11).

The results of the second method used to analyze winter severity (i.e., the area of the snow depth curve that is above the critical value) are summarized in Table 12. This method incorporates both the duration and the magnitude of critical snow depths. Because animals are probably more stressed by longer periods with snow not markedly above the critical depth than they are by shorter periods with snow far above the critical depth, this method is considered less effective for ranking winter severity than comparison of the duration of the periods of critical snow depth (Figure 18). On this basis, cows were stressed during seven and four of 15 years at Fort Chipewyan

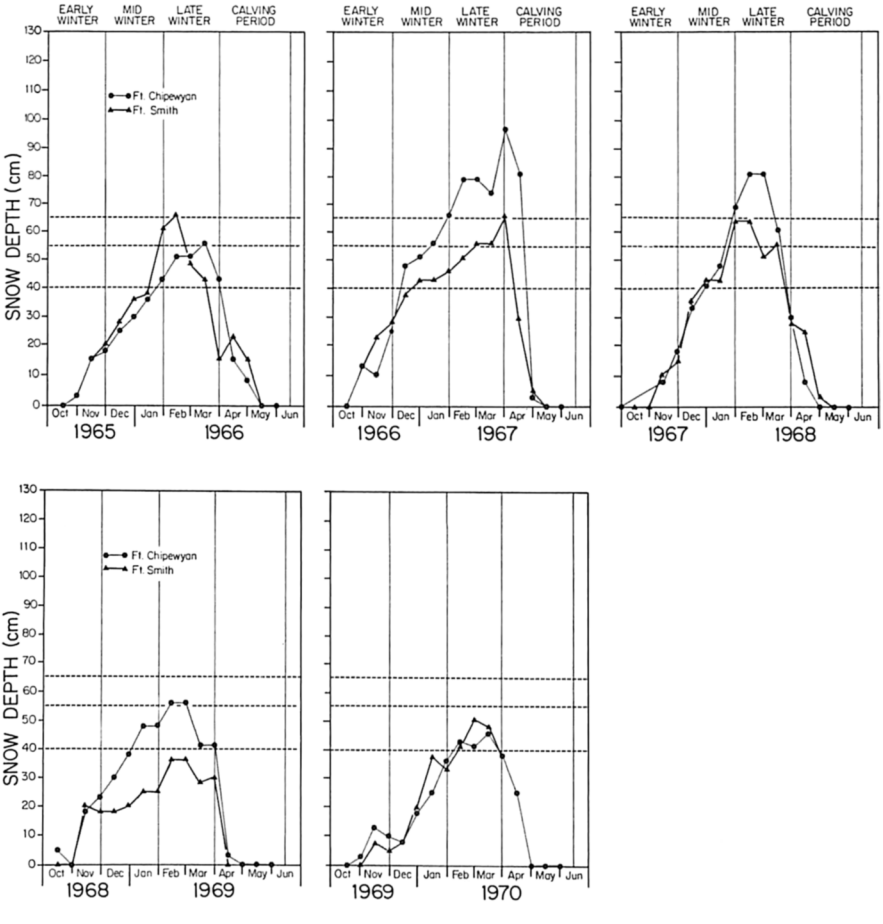


Figure 13. Snow depth values (cm) for Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1965/66 to 1969/70 (calculated from data provided by Alberta Environment). The dashed lines at 40,55, and 65 cm indicate the depth at which snow first becomes stressful to bison, the critical snow depth for calves, and the critical snow depth for adult males.

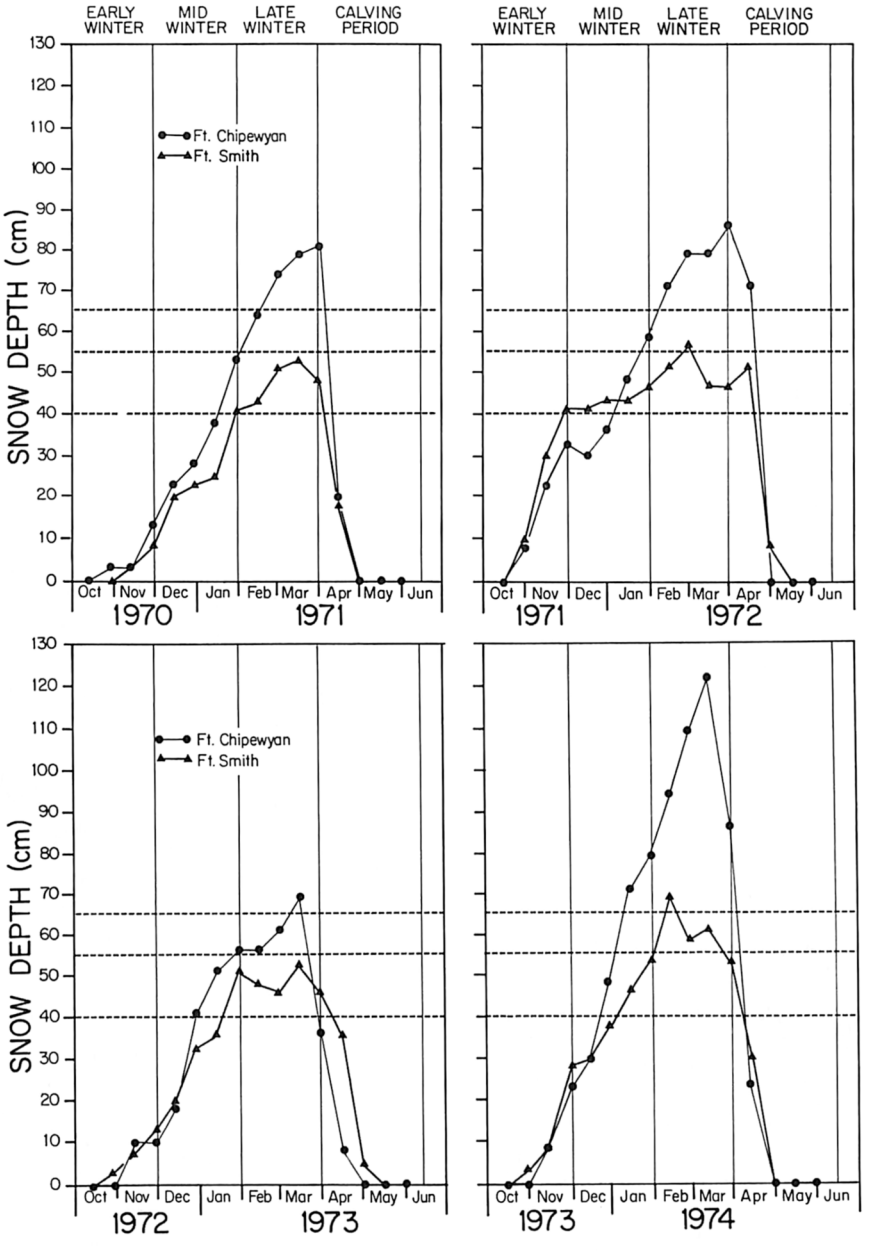


Figure 14. Snow depth values (cm) for Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1970/71 to 1973/74 (calculated from data provided by Alberta Environment). The dashed lines at 40,55, and 65 cm indicate the depth at which snow first becomes stressful to bison, the critical snow depth for calves, and the critical snow depth for adult males.

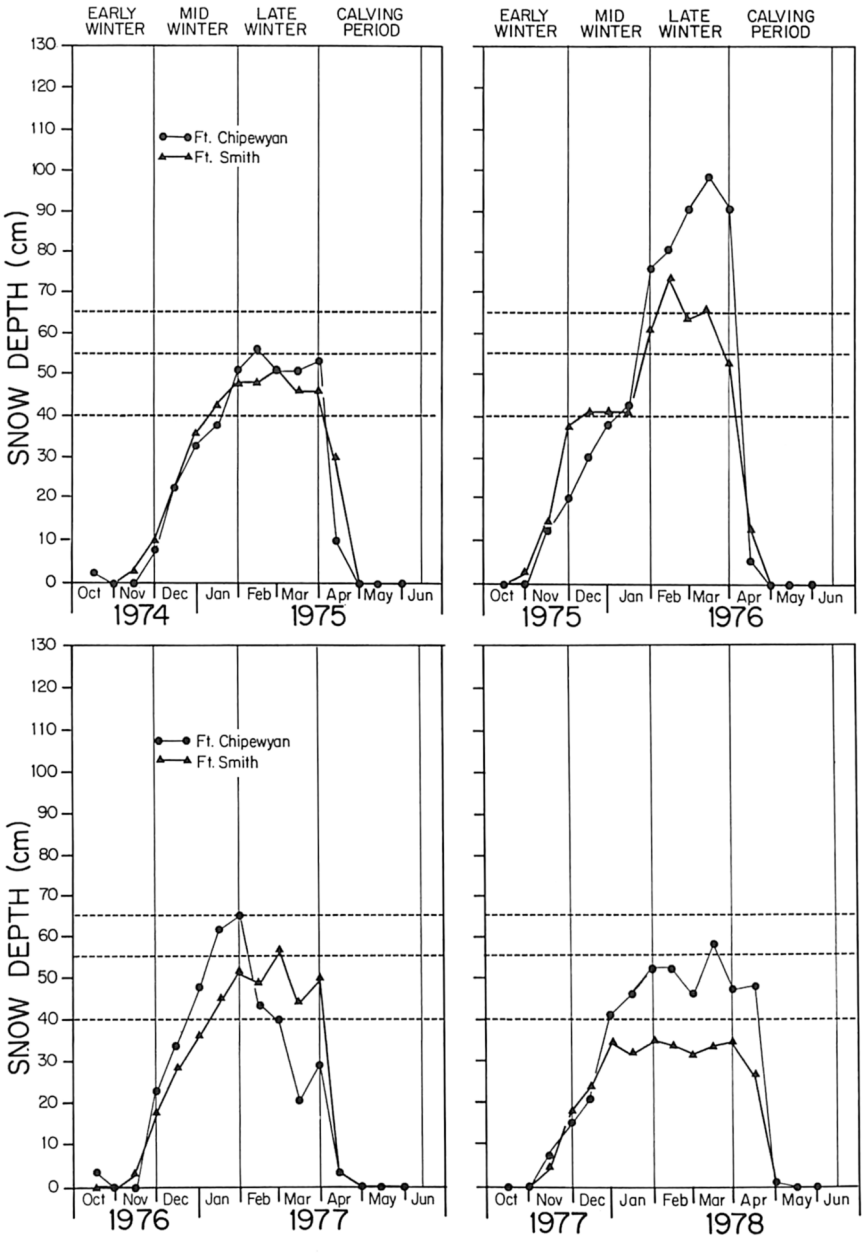


Figure 15. Snow depth values (cm) for Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1974/75 to 1977/78 (calculated from data provided by Alberta Environment). The dashed lines at 40,55, and 65 cm indicate the depth at which snow first becomes stressful to bison, the critical snow depth for calves, and the critical snow depth for adult males.

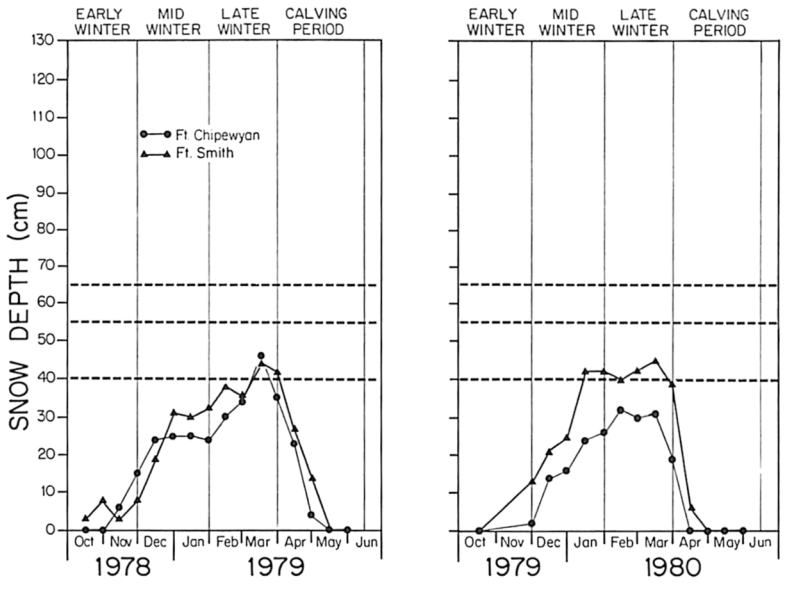


Figure 16. Snow depth values (cm) for Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1978/79 to 1979/80 (calculated from data provided by Alberta Environment). The dashed lines at 40,55, and 65 cm indicate the depth at which snow first becomes stressful to bison, the critical snow depth for calves, and the critical snow depth for adult males.

and Fort Smith respectively, while calves were stressed during 12 and seven of 15 years at these locations.

On the basis of snow depths greater than 55 cm (the critical snow depth for calves), the most severe winters occurred during 1966/67, followed by 1971/72 and 1975/76. The ranking of all years between 1970/71 and 1980/81 for Fort Chipewyan and Fort Smith is shown in Table 13.

After examining the data on the critical snow depth for adults (> 65 cm), we concluded that 1971/72, 1973/74, and 1975/76 were the most stressful winters for bison in the Delta, and that 1973/74 and 1975/76 were the most stressful for bison north of the Peace River (Figure 18). Considering the snow cover for the entire period from 1970/71 to 1980/81, one would predict lower calf production and yearling survival during the first five years than during the second five-year period. The aerial calf surveys were not precise enough to detect the effects on reproduction that may be due to differences in snow cover.

Our snow data analysis did not reveal anything that would allow us to tie the decline of the bison from 1971 to 1981 to specifics related to snow cover. If severe winters were to have caused declines, then the expectations are that benign winters would allow for increases. The impact of winter conditions is likely influenced through wolf predation.

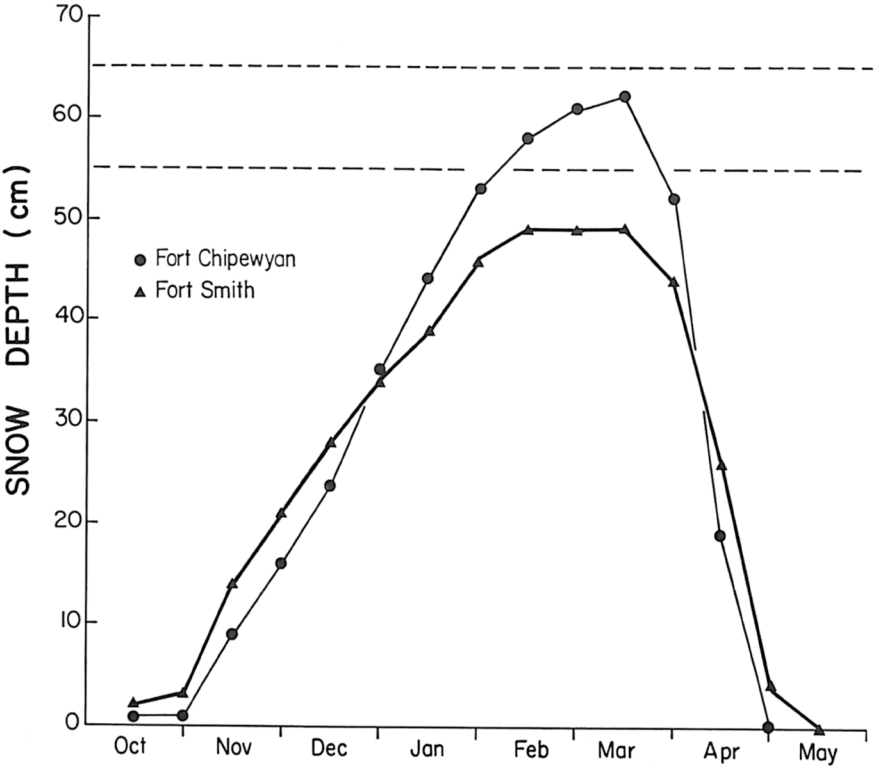


Figure 17. Long-term mean monthly snow depths at Fort Smith, N.W.T. (25 years), and Fort Chipewyan, Alberta (13 years). The dashed lines indicate the critical snow depths for calves (55 cm) and mature bison (65 cm).

C. *Temperature, Wind, and Windchill*

i) Introduction

Smaller ungulates, such as deer, experience significant heat loss when exposed to extreme cold and strong winds (Verme 1969, Ozoga and Gysel 1972, Moen 1976); they can conserve this energy by modifying their behaviour (e.g., seeking microenvironments that offer protection from winds and extremes in ambient temperature) (Moen 1968, Ozoga 1968, Lyon 1980), increasing insulation, and by reducing their metabolic rate (Silver et al. 1969, Seal et al. 1972, Moen 1978). Field observations of bison indicate that they modify their behaviour in response to low temperatures; according to Allison (1972), during midwinter (January and February), bison split into small herds and move into cover provided by forests, often leaving large, expansive meadows. Fuller's (1966) observations suggest that this behaviour occurs only when cold temperatures are coupled with moderate to strong winds. Wardens have observed

Table 10. Duration (in months) of the periods of critical snow depths (>55 cm), and rankings of winter severity at Fort Chipewyan, Alberta, and Fort Smith, N.W.T., 1965/66 to 1980/81.

	Fort Chipewyan, Alberta			Fort Smith, N.W.T.		
	Months	Rank (overall)	Rank 1970-81	Months	Rank (overall)	Rank 1970-81
1965/66	0.2	10	-	0.9	5	-
1966/67	3.2	1	-	1.3	3	-
1967/68	1.9	6	-	1.1	4	-
1968/69	0.5	8	-	0.0	8	-
1969/70	0.0	12	-	0.0	8	-
1970/71	2.1	5	4	0.0	8	5
1971/72	2.8	3	2	0.2	7	4
1972/73	1.9	6	5	0.0	8	5
1973/74	2.9	2	1	1.7	2	2
1974/75	0.3	9	7	0.0	8	5
1975/76	2.4	4	3	1.9	1	1
1976/77	0.9	7	6	0.3	6	3
1977/78	0.1	11	8	0.0	8	5
1978/79	0.0	12	9	0.0	8	5
1979/80	0.0	12	9	0.0	8	5
1980/81	0.0	12	9	0.0	8	5

Table 11. Number of years with higher-than-average and lower-than-average numbers of months with snow depths greater than 55 cm at Fort Chipewyan, Alberta, 1970/71 to 1980/81.

	Above long-term average (number of years)	Below long-term average (number of years)
Years of declining bison numbers (1970/71 to 1975/76)	5	1
Years of stable bison numbers (1976/77 to 1980/81)	1	4

Table 12. Ranking of winter severity using the area of the snow depth curve that is above the critical level (55 cm). Snow depth values are expressed as a percentage of the largest area recorded (1973/74 for Fort Chipewyan and 1975/76 for Fort Smith); zeroes indicate that the snow depth did not reach the critical level.

	Fort Chipewyan, Alberta			Fort Smith, N.W.T.		
Year	Relative area (%)	Rank (overall)	Rank 1970-81	Relative area (%)	Rank (overall)	Rank 1970-81
1965/66	0	9	-	25.0	3	-
1966/67	62.0	3	-	17.0	4	-
1967/68	29.0	6	-	25.0	3	-
1968/69	0	9	-	0	5	-
1969/70	0	9	-	0	5	-
1970/71	30.0	5	4	0	5	4
1971/72	44.0	4	3	0	5	4
1972/73	10.0	7	5	0	5	4
1973/74	100.0	1	1	58.0	2	2
1974/75	0.7	8	6	0	5	4
1975/76	63.0	2	2	100.0	1	1
1976/77	0.7	8	6	25.0	3	3
1977/78	0.7	8	6	0	5	4
1978/79	0	9	7	0	5	4
1979/80	0	9	7	0	5	4
1980/81	0	9	7	0	5	4

Table 13. Ranking of winter severity, on the basis of the duration of the period of critical snow depth (55 cm), at Fort Chipewyan, Alberta, and Fort Smith, N.W.T., 1970/71 to 1980/81.

Fort Chipewyan		Fort Smith	
Rank	Year	Rank	Year
1	73/74	1	75/76
2	71/72	2	73/74
3	75/76	3	76/77
4	70/71	4	71/72
5	72/73	-	-
6	76/77	5	76/77
7	74/75	5	74/75
8	77/78	5	77/78
9	78/79	5	78/79
10	79/80	-	-

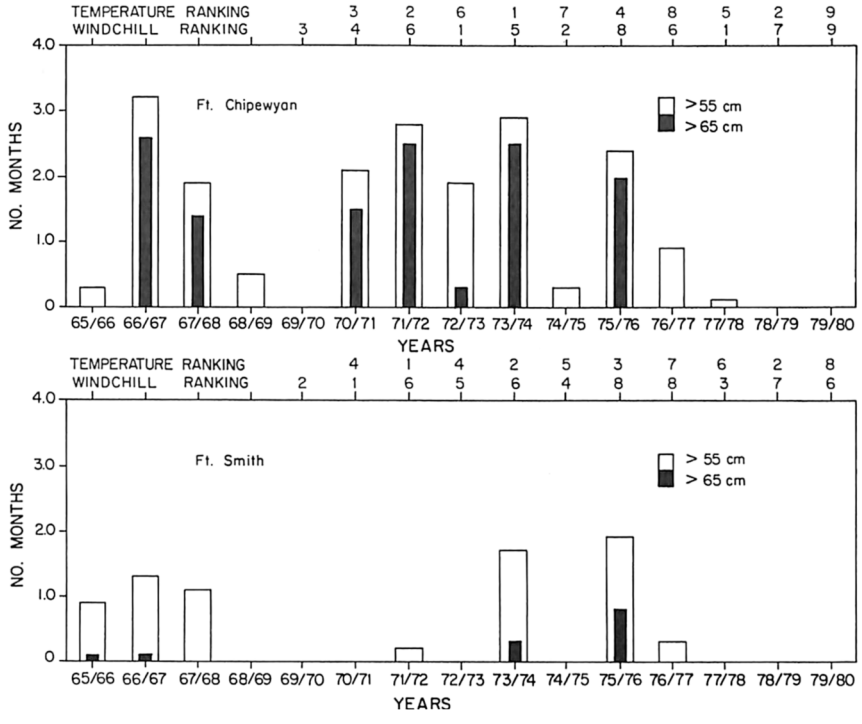


Figure 18. Duration (months) of the period of critical snow depth (55 cm for calves, 65 cm for adults) for each winter, 1965/66 to 1979/80, and comparison of winter severity using temperature and windchill values, 1970/71 to 1979/80, at Fort Chipewyan, Alberta, and Fort Smith, N.W.T.

that during late winter and early spring, bison often graze in meadows at midday when temperatures are higher. When the temperature falls during the evening, movement into shrubby or wooded areas occurs (D. Anions, field notes). Mautz (1978) and Flook (1970) found that the presence of fat reserves increases the chances of winter survival in deer and elk respectively. Along with the winter hair coat, these reserves also provide insulation against heat loss, and can be catabolized to compensate for the lower quality of forage on winter ranges.

Wind and low temperatures can affect the energy balance of an animal to the point at which, to survive, the body must compensate for these effects with metabolic adjustments. The temperature at which this response occurs (critical level) differs between species of mammals. Hart et al. (1961) measured the correlation between windchill values (the combined cooling effect of air temperature and wind velocity) and calf mortality in barren-ground caribou (*Rangifer tarandus*). Presumably windchill could also be used as an index of the cold stress experienced by bison. Christopherson et al. (1978) found that the metabolic rate of bison calves in a controlled-temperature chamber was actually lower at -30°C than at 0°C; this may

be an adaptive mechanism for conserving energy during winter, when food is less abundant. On the other hand, when bison calves were exposed to -30°C and a 4.7 km/hr wind, their metabolic rate rose above that measured at 0°C; the cold stress they experienced under these conditions forced them to increase their metabolic rate despite the resulting loss of energy (which probably occurs because wind disrupts the insulative value of the hair coat and increases the convective heat loss) (Christopherson et al. 1979). These results suggest that temperatures as low as -30°C, unless coupled with a wind, do not stress bison calves, and that an increase in the metabolic rate on exposure to cold is an indication of cold stress (Christopherson et al. 1979). The extent to which a given windchill value exceeds the value at a temperature of -30°C and a wind speed of 4.7 km/hr can probably be used as a measure of the intensity of cold stress experienced by bison calves.

Besides windchill, several other weather-related factors may play an important role in the energy balance of ungulates. These are:

1. Relative humidity, which may be important in the loss of body heat at near-freezing temperatures;
2. Evaporative cooling, which may occur if the body surface becomes wet;
3. Insulation provided by hair [bison hair has a higher insulative value than that of domestic cattle (Peters and Slen 1964)];
4. Solar radiation as a source of heat; and
5. The temperature of the body surface of ungulates, which may be different from the temperature of man's body surface (33°C), on which the windchill factor is based. A windchill equation specifically for bison could be constructed if the temperature of their body surface was known.

The objectives within this section are to:

1. Explore a possible relationship between windchill and winter severity;
2. Rank the severity of cold stress that is presumed to have been experienced by bison in the vicinity of Fort Smith and Fort Chipewyan during the winters between 1970/71 and 1980/81;
3. Determine whether the conditions experienced in the northern and southern portions of Wood Buffalo National Park are similar, by comparing the windchill factors at Fort Smith and Fort Chipewyan.
4. Compare the ranks assigned on the basis of windchill values with those assigned on the basis of snow-depth criteria to determine which method is most useful.

ii) Methods

Mean daily minimum temperatures recorded at Fort Chipewyan and Fort Smith for the winters between 1970/71 and 1979/80 were obtained from the Atmospheric Environment Service of Environment Canada in Edmonton.

A paired t-test was used to compare mean daily minimum temperatures for each winter between 1970/71 and 1979/80 at Fort Smith with those at Fort Chipewyan. A Mann-Whitney U-test was used to compare the severity of winter temperatures during the years of sharply declining numbers (1970/71 to 1975/76) with that of the winter temperatures recorded during the years of stable or slowly declining numbers (1976/77 to 1979/80).

Windchill factors were obtained from data supplied by the AES in Downsview, Ontario. The equation used by them to calculate windchill (H), expressed as watts/m^2, from air temperature and wind velocity is as follows:

$$H = 1.1625\ [\sqrt{(28V)} + 10.45 - 0.28V]\ (33 - T)$$

where V = wind velocity (km/hr) and T = temperature (°C).

The number of hours with a windchill above 1,500 watts/m^2 was calculated as a percentage of the total hours between 1 October and 31 March, then used as an index of the severity of the environmental conditions during each winter.

iii) Results and Discussion

Mean monthly temperatures are plotted in Figures 19 and 20; the long-term trends are shown in Figure 21. The threshold temperature (-30°C), below which the metabolic rate increases when there is a slight wind, is indicated on the figures. The data were summarized by Carbyn et al. 1989. At Fort Smith, the daily mean minimum temperature for the winters between 1970/71 and 1979/80 ($\overline{X}$ = -20.6°C) were significantly lower than those at Fort Chipewyan ($\overline{X}$ = -20.0°C) (paired t-test, 1-tailed; $p < 0.009$). Although this difference is statistically significant, it is probably not great enough to have much biological significance.

Winter temperatures during the years of sharply declining numbers were compared with the winter temperatures during the years of stable or more slowly declining numbers. During the decline, mean annual temperatures were usually lower than they were during the period in which the number of bison was more stable (Figures 19 and 20), but not significantly so (Fort Smith - U = 19.50, $p > 0.05$; Fort Chipewyan - U = 17, $p > 0.05$). During midwinter of four of the six years between 1971 and 1976, the mean monthly temperature was below -30°C. The mean monthly temperature was below -30°C during midwinter in only one of the four subsequent years (1977-1980). The mean daily minimum temperature may not be a good measure of the cold stress that is presumed to be experienced by bison because variations in conditions over a 24-hour period are not shown by this criterion. It is doubtful that temperature alone has much effect; it would have its greatest impact in combination with winds that create prolonged conditions of severe windchill, deep snow, and reduced availability of food.

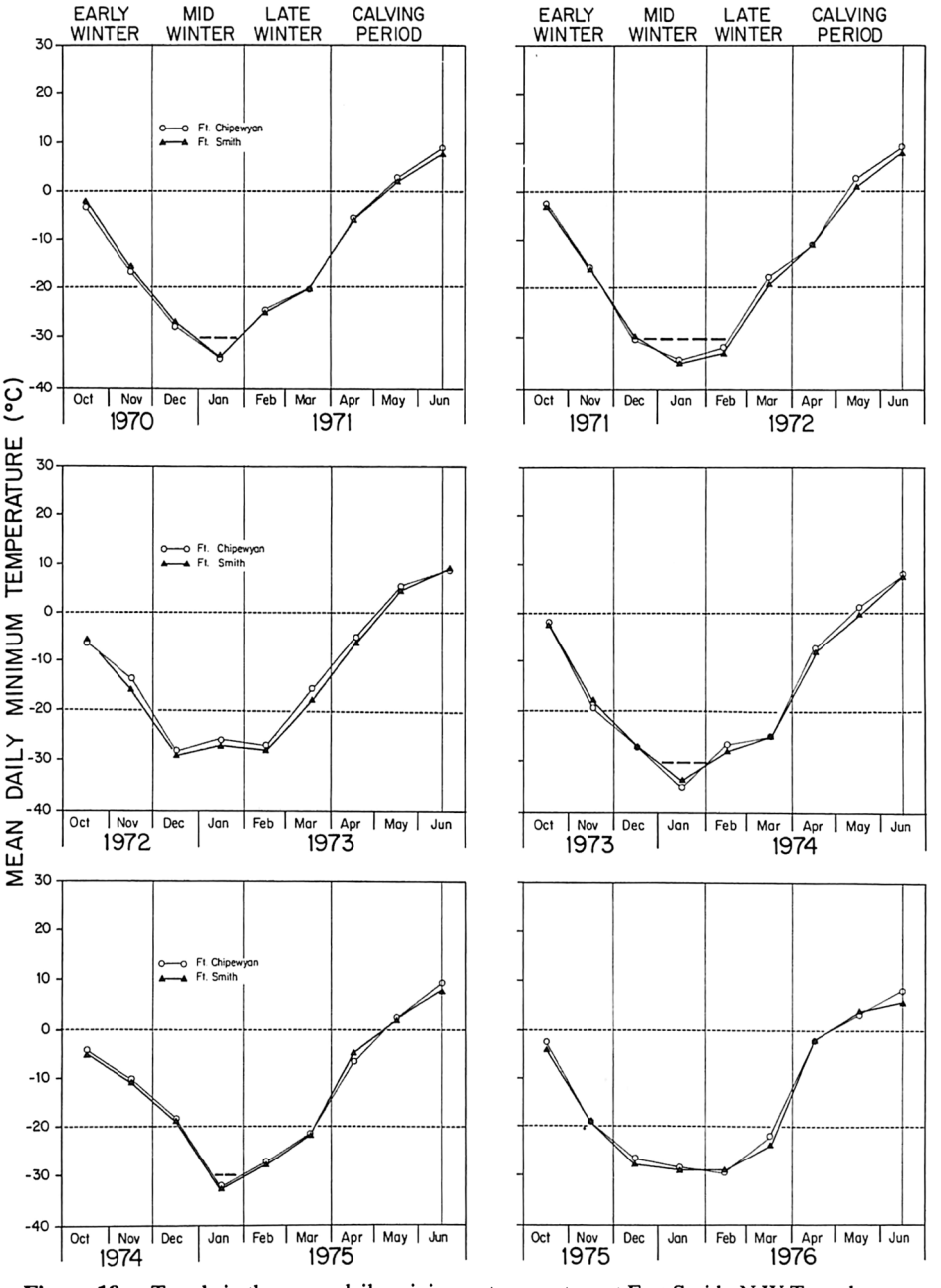


Figure 19. Trends in the mean daily minimum temperature at Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1970/71 to 1975/76. The dashed line at -20°C indicates the mean daily temperature in the study area during winter; the dashed line at -30°C indicates the temperature at which a bison calf can no longer maintain or reduce its metabolic rate in calm conditions.

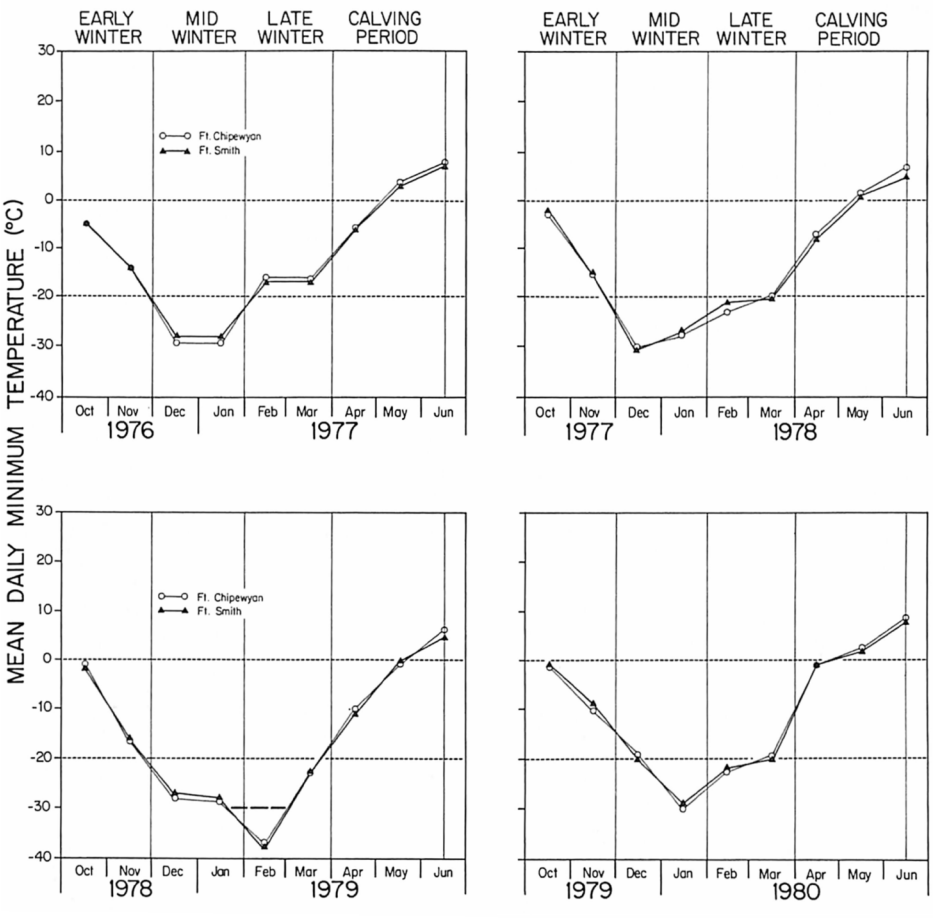


Figure 20. Trends in the mean daily minimum temperature at Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1976/77 to 1979/80. The dashed line at -20°C indicates the mean daily temperature in the study area during winter; the dashed line at -30°C indicates the temperature at which a bison calf can no longer maintain or reduce its metabolic rate in calm conditions.

A comparison of windchill values for each winter between 1970/71 and 1980/81 is shown in Table 14. Using mean minimum temperatures as the criterion, each winter was ranked in severity. As expected, there are differences between rankings derived by using actual temperatures and those derived using windchill values. However, there is a rough correlation between the two. The years of 1971/72 and 1973/74 were the coldest for Fort Smith and Fort Chipewyan respectively. The rankings derived by using windchill values and actual temperatures are shown in Figure 18 in relation to those derived using the duration of periods of critical snow depth. This method also

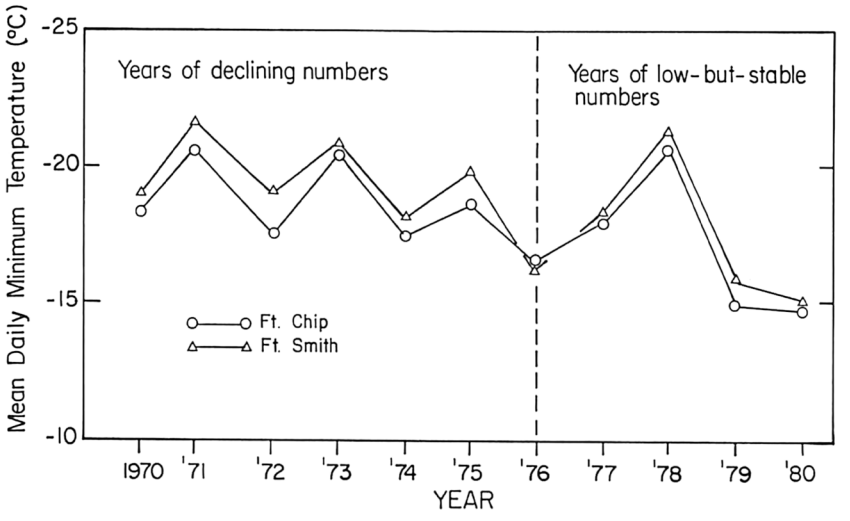


Figure 21. Generalized trends in mean minimum temperature for each winter (October-March), 1970-1980.

Table 14. The number of hours with a windchill greater than 1,500 watts/m^2 calculated as a percentage of the total hours between 1 October and 31 March, and ranks assigned according to temperature- and windchill-based values, at Fort Smith, N.W.T., and Fort Chipewyan, Alberta, 1970/71 to 1980/81.

	Fort Smith			Fort Chipewyan		
Year	% of total	Rank (windchill)	Rank (actual temp.)	% of total	Rank (windchill)	Rank (actual temp.)
1970/71	35	2	4	26	3	3
1971/72	39	1	1	24	4	2
1972/73	24	6	4	21	6	6
1973/74	29	5	2	30	1	1
1974/75	24	6	5	23	5	7
1975/76	33	4	3	27	2	4
1976/77	21	8	7	14	8	8
1977/78	21	8	6	21	6	5
1978/79	34	3	2	30	1	2
1979/80	23	7	8	18	7	9
1980/81	24	6	9	13	9	10

shows that winter conditions were more severe during the years of sharply declining numbers than during the years of stable or more slowly declining numbers, although the difference was not as pronounced as that indicated by the DPCSD (duration of critical snow depth method).

3. *Responses of Bison to Fire*

A. *Introduction*

Fire suppression has been an important management tool in Wood Buffalo National Park over the years. Special funds are available, which are separate from the operating budget. This flexibility is required in order to have resources available when needed. The extent of occurrence of fire in the Park varies considerably from year to year (Figure 22), therefore its impact on bison varies over time. Opportunistic observations, made by wardens, on the responses of bison to fire and to newly burned areas are summarized in this section.

Between 1979 and 1981, a much higher than average number of major fires spread over large areas in and around Wood Buffalo National Park (Figure 22). Most of these fires occurred north of the Peace River, but some did occur in the southern part of the Park (Peace-Athabasca Delta), where the majority of bison and bison range were (at that time) and still are found. Because frequency of fires is lowest in the part of the Park that contains the most bison and range, the hydrological regime of the Delta is probably more important than fire to this area, and thus to the total bison population of the Park. However, there is undoubtedly a link between the two components. Fires influence the composition of plant communities and contribute to the recycling of organic matter; presumably those processes are enhanced during years of drought, when fires are more common. Fires also generally promote the expansion of new grasslands while retarding the invasion into existing grasslands by woody plants (Holsworth 1960).

B. *Methods*

During aerial surveys, Park wardens have recorded casual observations of the responses of bison to newly-burned ranges and the direct responses of bison to fires burning through forested areas. Some of them have been summarized below.

C. *Results and Discussion*

After the fire season during 1971, wardens reported a number of responses by bison to specific burns. In November 1972, approximately 150 bison were seen feeding in an area along the Nyarling and Little Buffalo Rivers that had been burned during the previous summer (Stewart 1972). Extensive fires that occurred north and west of McNeil Lake during 1971 could have led to greater use of the range there; by 1974, it appeared that bison had increased their use of the area (Cooper 1975), and several herds spent the summer (from 15 May - 10 September 1975 at McNeil

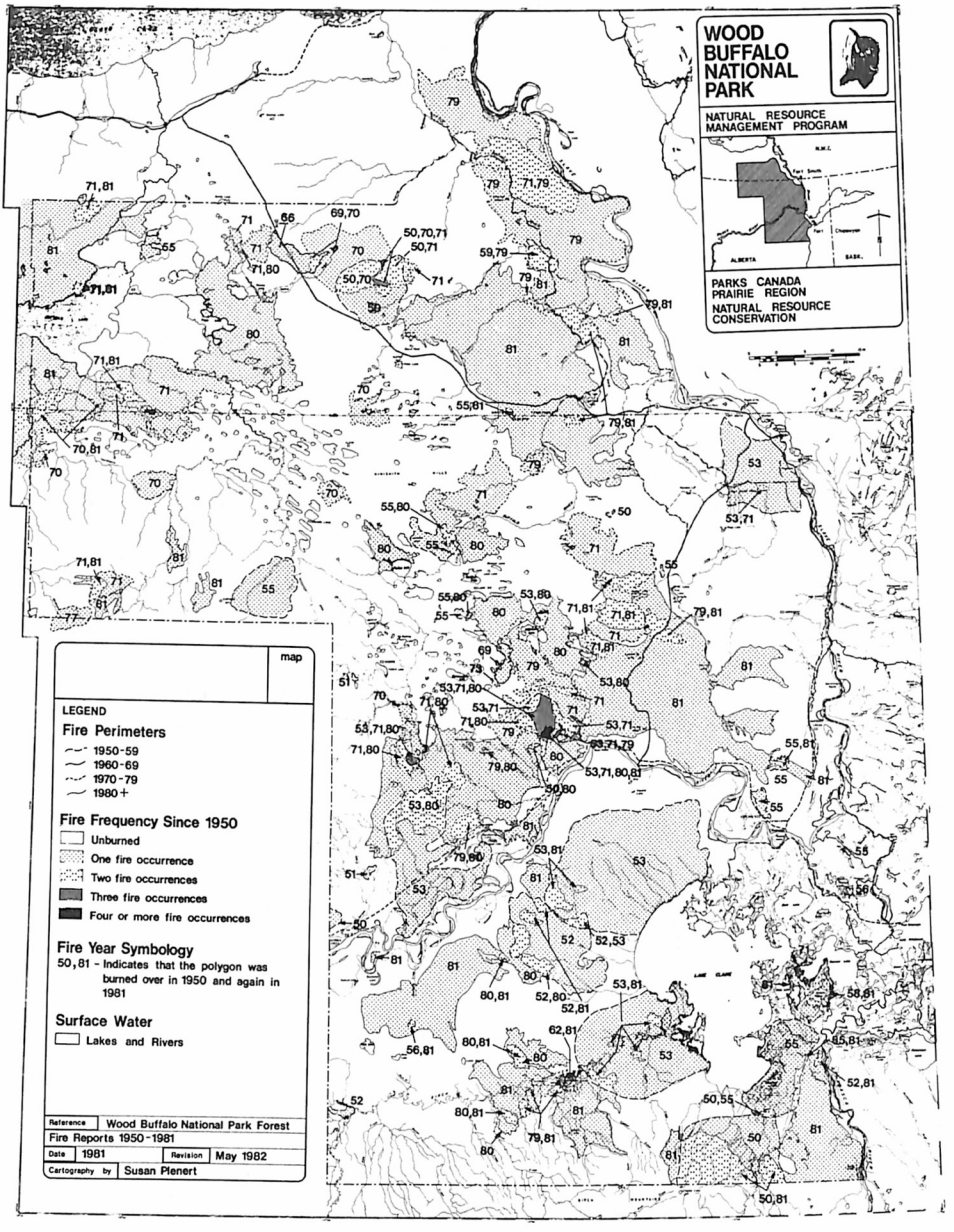


Figure 22. Overview of the fire history of Wood Buffalo National Park, from 1951-1981 (from WBNP Resource Description Analysis).

Lake). No similar concentrations were subsequently observed there, perhaps because this new range had been overgrazed (D. Anions, unpubl. data).

During the summers of 1979, 1980, and 1981, several large fires north of the Peace River (Area I) affected bison range in the Park. For instance, during June and July of 1980, a fire east of the Caribou Mountains burned an extensive area; bison used a burned area within the limit of this fire during 1981. Bison were also seen during that year in a burned area adjacent to Jackfish Creek, and signs indicated that they were probably feeding nearby (D. Anions, field notes). One of the most important burned regions in Area I lies between Peace Point in the south and Pine Lake in the north, where large areas of jack pine, black spruce, and poplar forest were burned during July and August of 1981; during anthrax surveillance surveys conducted in the summers of 1982 and 1983, herds of bison were regularly observed grazing within part of this burned area (D. Anions, field notes). In 1983, E. Kuyt (pers. comm.) noted the increased use by bison of an area near Seton Creek that had been burned during 1981.

Fires may also cause bison to desert a region that they have previously used on a consistent basis. In Area II (south of the Peace River), a fire during August 1981 burned a large area of sedge meadow west of Lake Claire. Few bison were found in the area during the total-count survey in March 1982, although it had been used extensively by large herds in previous years (Fremont and Bell 1982). They may have moved to other ranges because the sedge meadows had not yet recovered from the fire.

Changes in movement patterns that have been observed within Area I may also be attributed to fires. Fall migration on the trail between Raup Lake and Hay Camp Meadows has been less pronounced during the mid 1980s; it appears to have been replaced by movements southward through the area that was burned during 1981 and toward Peace Point and Carlson's Landing. Inspection of the ranges near Raup Lake (D. Anions, 11 July 1983, field notes) indicated that there had been little use of the area since the fire, and that the range appeared to be in excellent condition. The traditional use of ranges and movements by bison may well be influenced by fires; however, the observed abandonment of some areas could also be the direct result of declining numbers.

There have been few reports of behavioral responses of bison to fires while they are burning. Singer et al. (1989) reported that during intense forest fires nine bison were killed in 1988 in Yellowstone National Park. It appears that in less intense fires, bison are not greatly disturbed and merely wander away as one approaches (G. Mason, pers. comm.). In one instance, firefighters reported that a bison slightly burned its feet while walking through an area that had recently been burned (G. Mason, pers. comm.). Fires are not considered to be an important cause of bison mortality. Bison regularly travel traditional trails along ridges; observations indicate that these trails are used immediately after fires. There is some speculation that the incidence of biting insects may be reduced in burned areas, which are more open, and that this may contribute to the increased use of these areas by bison.

IV Bison Population Parameters

The dynamics of populations are determined by four factors — natality, mortality, emigration, and immigration. Since emigration and immigration of bison across the boundaries of Wood Buffalo National Park appear to be negligible, major changes in the bison population depend on the relationship between natality and mortality. Analysis indicates that the bison population began to decline during the early 1970s and that the initial decline from a previous high was accelerated by a high rate of mortality (drowning) during 1974. In order for the population to regain its former abundance, birth rates and recruitment would have to exceed mortality.

A large body of data was collected by the wardens on their aerial surveys from 1971 to 1991. The most intensive work was carried out in the first decade of the 20-year period. Surveys to monitor bison concentrations and movements, anthrax surveillance counts, total counts (late winter), calf counts (periodic), and smoke patrols were part of the wardens' responsibilities in resource conservation. The synthesis of the data collected during these surveys is discussed under six headings — total counts and population trends, bison concentration counts, migration and movement, anthrax surveillance, herd-size dynamics and calf surveys.

1. *Total Counts And Population Trends*

A. *Introduction*

Prior to 1970, Oldham, Fuller and Novakowski conducted aerial surveys at irregular intervals to count bison over small portions of the Park. These surveys provided rough estimates of bison abundance and were considered to be an inadequate means of counting bison (Soper 1941, Fuller 1950). Wardens began conducting aerial surveys on a regular basis during the winter of 1970/71. At that time, concern over the long-term effects of the Bennett Dam on the Delta's hydrological regime prompted the initiation of more frequent, systematic, and widespread efforts to monitor changes in the distribution and abundance of bison. It was not until 1975 that warden surveys routinely included secondary ranges and methods became standardized.

B. *Methods*

Total-count surveys were conducted once per year — in February — between 1971 and 1975, and after 1975 during March. Surveys were conducted using randomized flight patterns covering 100% of the primary areas whereby all bison within specific areas were systematically counted and their locations plotted on topographical maps (usually a scale of 1:250,000). Area I (north of the Peace River) and Area II (south of the Peace River) subsets of primary (P) and secondary (S) ranges were identified on the basis of known bison distribution. Primary ranges are areas that are consistently used by bison during the winter and are also used to a large extent during summer; they were divided into zones. Secondary ranges receive intermittent use and are rarely frequented by large herds on a regular basis. A fixed-wing aircraft, usually a Cessna 185, was used for aerial surveys. Flying altitude varied between 244 m and 370 m above ground level. A modified grid pattern was flown over areas of known concentration. At least two observers were present on each flight to count and record numbers, and photographs were taken to aid in counting large herds. Environmental conditions and the particulars of each flight were recorded on standardized forms. The duration of each flight was usually three to five hours per day.

From 1971 to 1974 total-count surveys were largely restricted to primary ranges; from 1975 to the present they have covered all known primary and secondary ranges. To obtain estimates of the number of bison on secondary ranges between 1971 and 1974, a correction factor of 13.3% (Stelfox and Kingsley 1975) was applied to the data.

Movement and concentration counts, which were largely restricted to primary ranges, were conducted regularly between 1971 and 1979; after 1979 these were conducted only at irregular intervals. During some years, better results were obtained from surveys that monitored movements and concentration counts than from total-count surveys. In this event, wardens used the results from the former to obtain population estimates.

Each year, preliminary flights were usually made over primary ranges to assess major concentrations and to assess the amount of effort that would be required for total counts per zone or area. In addition, the specific level of coverage required in each area was usually discussed between the navigator (coordinator) and the pilot before takeoff on each day of a survey.

The program's coordinators monitored the weather patterns before each flight to determine whether flying conditions were suitable. The optimum environmental conditions for conducting surveys are clear, calm days with temperatures between -10°C and -20°C. During winter, high-overcast conditions are preferable to bright sunshine. Ideally, wind velocities should not exceed 16 km per hour. Although survey crews were well aware of these criteria, it was not always possible to complete surveys while conditions remained ideal.

The use of binoculars is not mentioned in the reports for surveys conducted between 1975 and 1979; however, they were used periodically by some observers.

Binoculars were used on total-count flights after 1980. Small (7 x 35) Leitz compact-type binoculars were preferred because they are easier to hold steady and get close to the airplane's windows for a downward view. Mini-cassette recorders were used in surveys of Areas I and II during 1978 (Couchie and Collingwood 1978) and in Area II during 1981. After a decade of intensive surveys in the 1970s, total counts were continued on an annual basis during the 1980s, except during 1982 (surveys were incomplete) and 1986 (no surveys were conducted).

Flying speeds varied from 128-208 km/hr, depending on the terrain, vegetation cover, and bison concentrations (Couchie and Collingwood 1978). When bison were located, the plane circled the area and two observers (occasionally three) counted the animals and plotted the results on maps. The aircraft was slowed as much as possible during circling and counting.

East-west transects were flown over primary ranges during most total-count surveys. However, transects were usually not evenly spaced or parallel, but were spaced in such a way that traditional ranges and open areas known to be heavily used by bison were covered. The flight pattern also varied with the topography, visibility, and the type of cover. Millette and Collingwood (1977) referred to this pattern as a "modified grid system" or the "spaghetti pattern". Accuracy with which the pattern was flown depended to a large extent on the navigator's knowledge of the area and his skill and experience in directing the pilot. Over secondary ranges, the flight lines were more widely spread than over primary ranges. Over both types of range, flight lines might be irregular so that small prairies, sedge meadows, and lake edges could be searched.

Between 1975 and 1991, the results were usually recorded directly on a topographic map; wardens occasionally used reference numbers to record for Area II. This was necessary when too many bison were concentrated in a small area.

The first year during which an attempt was made to consistently and carefully record results in a table (as well as on a map) was 1980 (Anions and Lukiwski 1980). One observer recorded all data called out to him by the navigator, pilot, and observers. Soon after the flight, the results were checked and tabulated.

Herds larger than 20-30 animals were generally photographed using a Nikon F-2 camera equipped with a motor drive and a 135 mm lens. At low temperatures this was not possible because the airplane's windows frosted over. In order to evaluate the precision of the methods employed, four separate counts were made, between 1972 and 1975, of the bison on each range during midwinter and the results were compared. The highest figure obtained for each range was considered to be the best count and was used for statistical analyses.

Much of the experience gained by wardens during the 1970s was applied during the total-count surveys conducted during the 1980s. Some aspects such as flight patterns were modified as the technique became more standardized. Except during 1987, the participants in a given year were the same throughout that year. On each day, counts were made for approximately two to three hours in the morning, followed by a two-hour break (to reduce fatigue), after which counts were

made for another two to three hours. Since 1985, the total flying time/year has varied from 29-35 hours. Flight lines were marked on maps, and at the end of each day, the survey was terminated at a convenient location over secondary range where bison were known not to be numerous. Thus, surveyors avoided counting the same bison on two different days.

C. *Results And Discussion*

The data collected during the wardens' surveys conducted between 1971 and 1981 were extensive. More than 23,000 entries were collected by at least 48 investigators during more than 2,000 man-hours of flying time. Total count flights from 1981 to 1991 resulted in an additional 924 flying hours.

The number of bison counted during censuses conducted between 1971 to 1991 (Table 15) have been summarized. Trends in the population's size are shown in Figures 23 and 24. Between 1975 and 1991, the mean number of bison on secondary ranges for Area I was 35% of the number on primary ranges, and for Area II, 9%. The overall average was 78% on primary range and 22% on secondary ranges. In order to obtain comparable estimates for 1971-1974, the number of bison counted on primary ranges each year was multiplied by 13.3 to produce an estimate of the total number. An underlying assumption when using this correction factor is that the same proportion of bison use primary ranges when there are 5,000 bison in the population as when there are 10,000.

Although some variation existed between years the results did show a trend. In some cases, differences can be attributed to the survey's design. For example, the low figure obtained during 1980 for the secondary range in Area II was attributed to the lack of familiarity of the navigator and observers with the region (Anions and Fremont 1981). This poor survey resulted in the dropping of the figure in some of the calculations.

Calculations for the ratio of bison in primary and secondary ranges were carried out for data collected from 1975 to 1991. The primary ranges in both areas contain the majority of the bison in winter — 65% in Area I (north of the Peace River) and 91% in Area II (south of the Peace River). The relationship between the number of bison on primary ranges and the number on secondary ranges from 1975 to 1981 was examined using Spearman's rank correlation (Figures 25 and 26), but no significant correlation ($p > 0.05$) was found for either Area I ($r = 0.280$) or Area II ($r = 0.046$). This shows that when the number on the primary ranges within each area increases or decreases, there is not a statistically significant reciprocal decrease or increase on the secondary ranges. There was a hint of an inverse relationship between the number of bison on primary ranges in Area I and the number on primary ranges in Area II (Figure 27), but this was not statistically significant (1-tailed t-test; $r = -0.0668$, $p > 0.05$). This suggests that some exchanges between primary ranges in Areas I and II do occur and that the exchange is probably determined by external factors, rather than by intrinsic behavioral responses. For example, ground observations of movement

Table 15. Number of bison recorded during total count surveys on primary and secondary ranges in Wood Buffalo National Park 1971 to 1991. Figures in brackets denote % of total. There was no survey in 1982 and 1986.

Year	Area I		Area II		Total	Confidence Limits	S E
	Primary	Secondary	Primary	Secondary			
1971	-	-	-	-	10832	-	-
1972	-	-	-	-	10491	-	-
1973	-	-	-	-	9134	-	-
1974	-	-	-	-	8401	-	-
1975	1428 (83%)	290 (17%)	3351 (88%)	458 (12%)	5527	5218-5836	309
1976	627 (74%)	227 (26%)	4967 (95%)	240 (5%)	6061	5745-6378	317
1977	1260 (78%)	365 (22%)	3440 (97%)	105 (3%)	5170	4876-5464	294
1978	1083 (77%)	314 (23%)	3602 (91%)	374 (9%)	5378	5067-5679	306
1979	989 (65%)	543 (35%)	3631 (91%)	376 (9%)	5539	5224-5854	315
1980	704 (68%)	330 (32%)	3450 (99%)	28 (1%)	4521[1]	4264-4778	257
1981	1279 (73%)	479 (27%)	3503 (92%)	303 (8%)	5558	5242-5874	316
1983	958 (65%)	507 (35%)	3471 (98%)	70 (2%)	5006	4721-5291	285
1984	842 (52%)	779 (48%)	2418 (79%)	628 (21%)	4667	4401-4933	266
1985	272 (22%)	994 (78%)	2860 (85%)	506 (15%)	4582	4321-4843	261
1987	540 (35%)	1015 (65%)	2218 (86%)	366 (14%)	4139	3903-4375	236
1988	506 (57%)	378 (43%)	2642 (81%)	604 (19%)	4130	3895-4365	235
1989	455 (39%)	706 (61%)	1947 (93%)	146 (7%)	3254	3069-3439	185
1990	1460 (93%)	114 (7%)	1710 (95%)	91 (5%)	3375	3181-3567	192
1991	1392 (89%)	172 (11%)	1642 (94%)	104 (6%)	3310	3122-3498	188

Area I: Average Primary = 65%; Average Secondary = 35%.
Area II: Average Primary = 91%; Average Secondary = 9%.

[1] Poor survey.

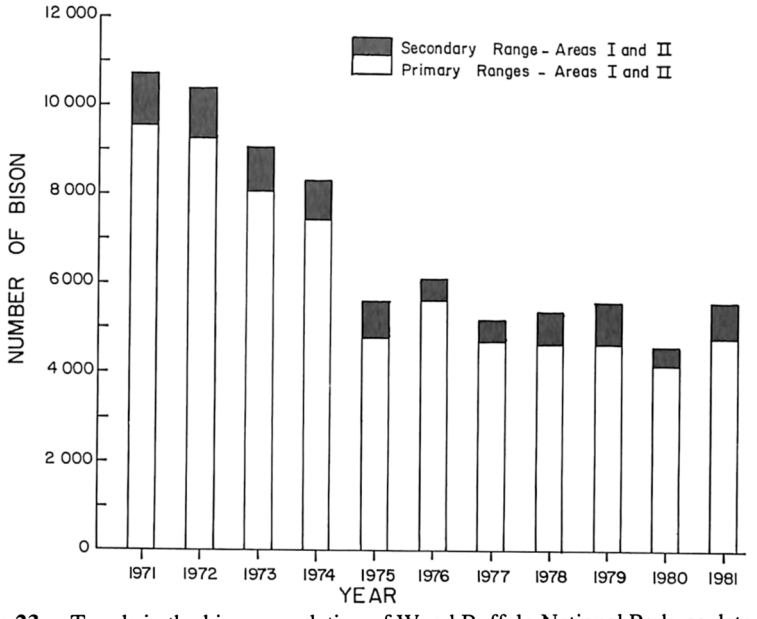


Figure 23. Trends in the bison population of Wood Buffalo National Park, as determined from wardens' surveys, 1971-1981. For the period from 1971 to 1974, estimates for secondary ranges were obtained by calculating 13.3% of the number on primary ranges (after Stelfox and Kingsley 1975).

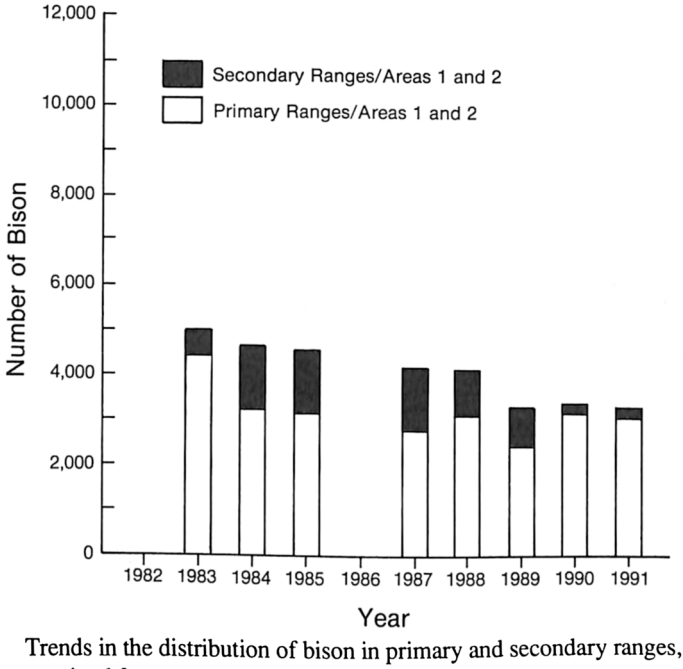


Figure 24. Trends in the distribution of bison in primary and secondary ranges, as determined from wardens' surveys, 1982 to 1991.

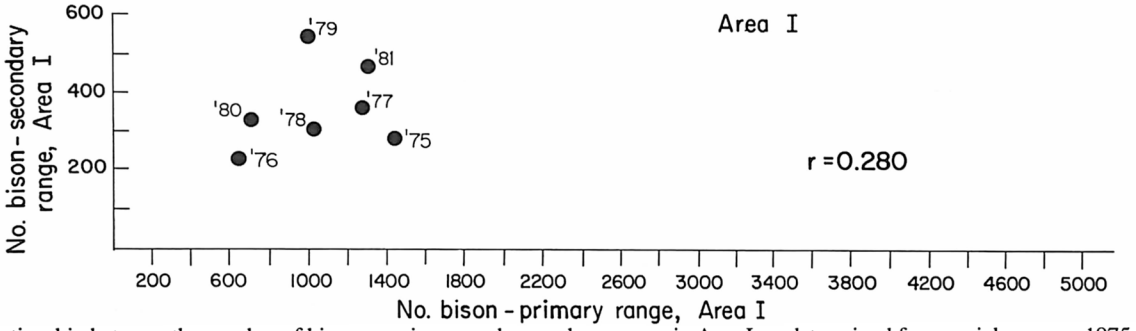


Figure 25. Relationship between the number of bison on primary and secondary ranges in Area I, as determined from aerial surveys, 1975-1981.

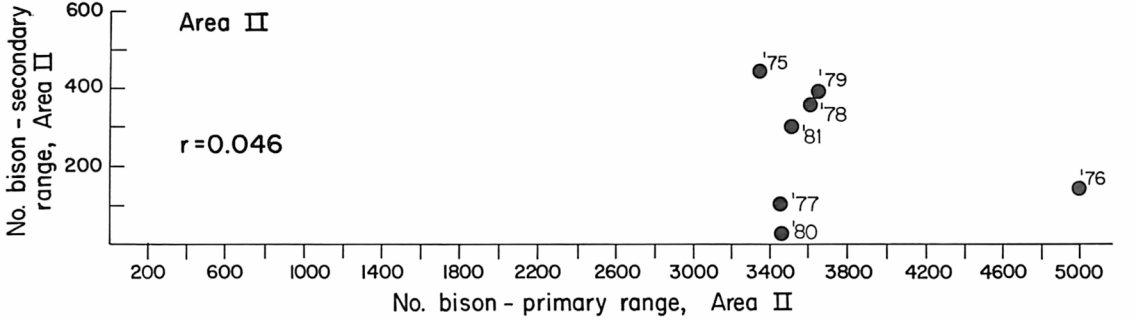


Figure 26. Relationship between the number of bison in primary and secondary ranges of Area II, as determined from aerial surveys, 1975-1981.

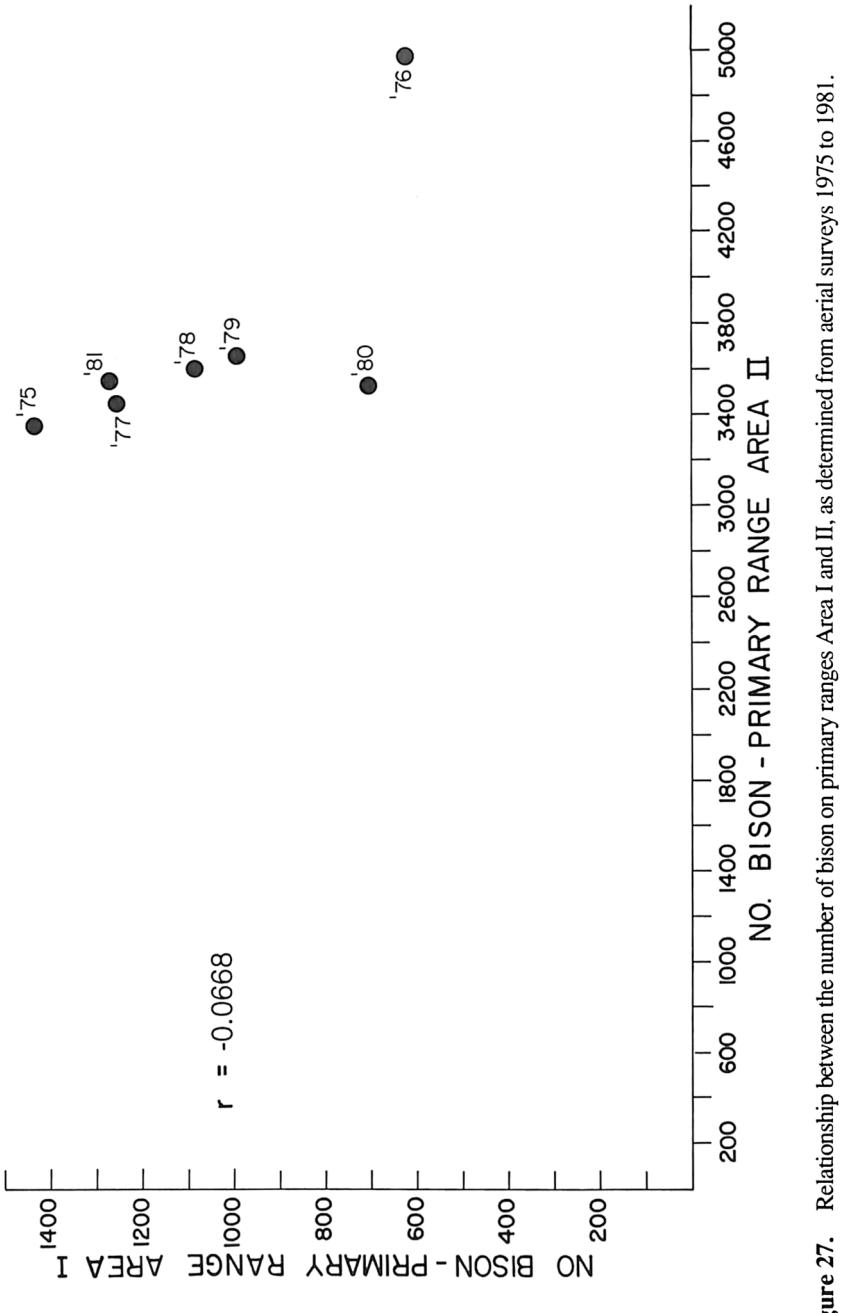


Figure 27. Relationship between the number of bison on primary ranges Area I and II, as determined from aerial surveys 1975 to 1981.

patterns of bison in one portion of the Delta varied considerably from the fall of 1991 to the fall of 1992. Furthermore, it appears that these movements are not long-term displacements, but short in duration. That is, the bison move back and forth, but numbers generally return to the same north/south ratio as before. One of the most dramatic examples of such an exchange was seen on 27 March 1973 when 880 bison suddenly appeared on Murdock Creek Meadows. They probably came from the vicinity of Egg Lake, south of the Peace River. There was no apparent cause for this mass movement. This shift was short lived, as by the next year proportions of bison in north/south distribution was similar to that of ratios prior to the 27 March 1973 shift. Similarly in January 1976 a southward movement of approximately 1,000 bison was recorded, and a large proportion of those animals (numbers not recorded) moved north in April 1976. If shifts were predictable, one would expect a consistent pattern. Because the bison population has recently declined from much higher levels, it is possible that primary ranges are not currently stocked at maximum levels, and that the presence of bison on secondary ranges is the result of either traditional use of marginal ranges or is dictated by variable external factors such as fire, predation, and fluctuations in the water level.

The conclusions that we have come to on the basis of survey information is supported by the preliminary results available from radio-tracking data (Van Camp et al. 1991). They monitored 33 radio-tagged bison that were relocated 377 times from August 1990 to March 1991. Their preliminary conclusions were that there did not appear to be free mixing of animals on the different ranges.

Twenty-year changes in the number of bison in Areas I and II (Table 16) show that the percentage of bison in Area I, when compared to the total population, increased from 1971 to 1991. In the 1971-1976 period the population north of the river was about 15% of the total Park population while in the 1986-1991 period the northern population represented 38% of the total Park population. A 5-year average progression of 12% (1974), 29% (1980), 33% (1987) and 38% (1991) shows the trend. Essentially, the population north of the river was stable to slightly declining, while south of the river the population declined significantly. The year after the 1974 flood in Area II, bison numbers increased in Area I, but then numbers declined in the second year after the flood (Table 16). As expected, the relationship was reciprocal in Area II. Because 85% of the total population was in Area II, the overall effect was a decline.

Percentage calculations are less revealing than a regression analysis (Figure 28). Decline south of the Peace River (Area II) was exponential ($(Ln(y) = 8.939 - 0.071t$, $r^2 = 0.844$ or $y = 7624 - e^{0.071t}$) while for Area I there was no trend ($(Ln(y) = 7.210 + 0.001t$ or $y = 1353 + e^{0.001t}$). If 1974 is treated as an aberration because of the high mortality relating to the flood, and if the next few years are treated as a recovery, then they may be eliminated from the regression. The new regression (Figure 29) explains about 10% more of the variance than does the original. This suggests that, following the perturbation and recovery, the population resumed its decline at the same rate as before the flood (Figure 29); $r^2 = 0.959$; $y = 9.137 -$

Table 16. Comparison of bison survey results in Areas I and II from 1971 to 1991. AI/T is percentage of Area I over total population.

Year	Area I	Area II	AI/T	Total
1971	2088	8744	(19%)	10832
1972	1228	9263	(12%)	10491
1973	1072	8062	(12%)	9134
1974	986	7415	(12%)	8401
1975	1718	3809	(31%)	5527
1976	854[1]	5207	(17%)	6061
1977	1625	3545	(31%)	5170
1978	1397	3981	(26%)	5378
1979	1532	4007	(28%)	5539
1980	1071	3450	(29%)	4521
1981	2061	3497	(37%)	5558
1982	-	-	-	-
1983	1465	3541	(29%)	5006
1984	1621	3046	(35%)	4667
1985	1216	3366	(27%)	4582
1986	-	-	-	-
1987	1555	2584	(33%)	4139
1988	884	3246	(21%)	4130
1989	1161	2093	(36%)	3254
1990	1574	1801	(47%)	3375
1991	1564	1746	(38%)	3310

[1] Southward movement of ± 1,000 bison in January; return migration in April (number not specified) was documented to account for this change. Survey was conducted in March. Readjustments in the proportions were noted to have taken place by the March, 1977 surveys.

0.080t. Whatever factors are operational in Area II are not equally important in Area I. The significance of these observations are discussed in other chapters.

The key may be an analysis of habitat differences between Areas I and II. An understanding is needed on how much of the primary ranges of bison were lost from 1971 to 1991. Bison numbers decreased by a factor of 3.2 while satellite imagery shows an approximate loss of ranges by a factor of 2.

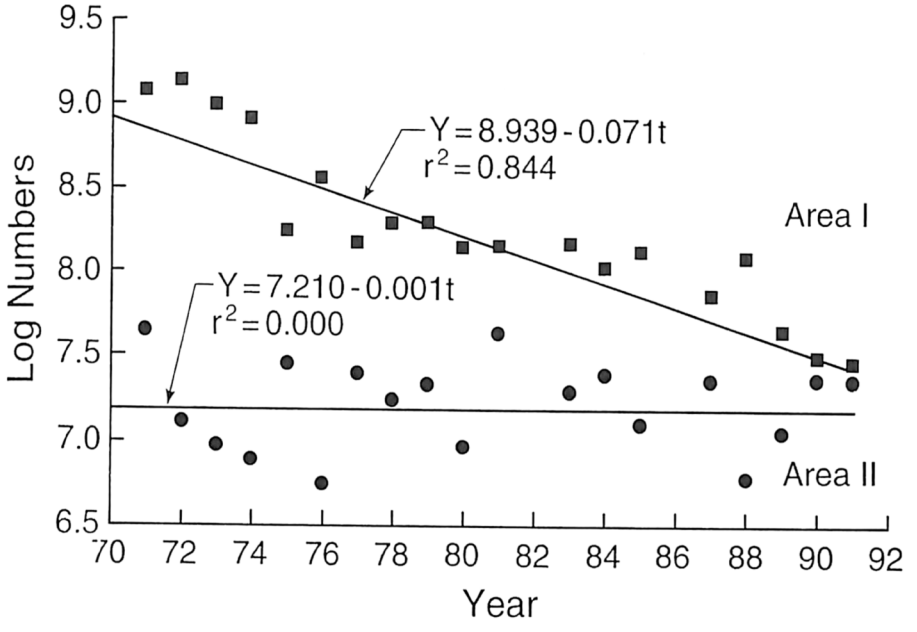


Figure 28. Bison population changes from 1971 to 1991, in Areas I and II shown seperately.

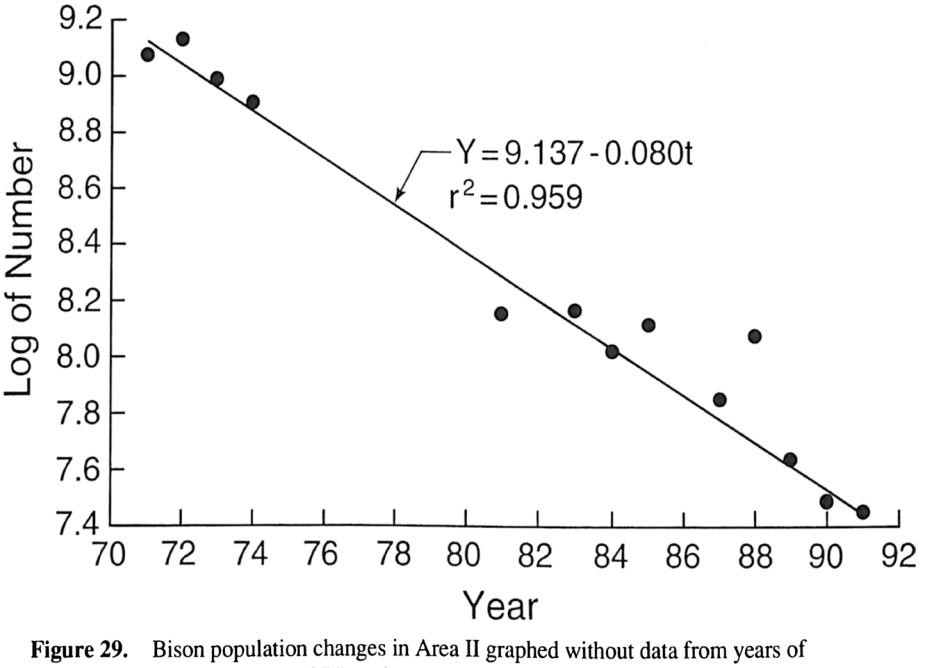


Figure 29. Bison population changes in Area II graphed without data from years of drastic decline (1974) and years of stable numbers (1975-1980).

2. *Bison Concentration Counts*

A. *Introduction*

Early in the 1970s, wardens conducted surveys to determine where bison were concentrated to set the stage for intensive management programs. The results were to be used for the locations of corrals in proposed expansion of vaccination programs. A report by Tempany and Cooper (1975b) outlines migration routes and documents the changes in concentration, by zones, for the years between 1970 and 1975. Up to 1975, approximately 150 surveys were completed. The effort was most intensive during 1974 and 1975, when at least 83 surveys were completed. Two wardens were then heavily involved in the bison research program at all times, and most other staff members were involved to some degree.

Surveys were conducted less frequently once the corrals' locations were approved. Approximately 45 total-count and migration surveys were conducted between 1976 and 1979 (Carbyn et al. 1989). During April 1979, at a meeting of the Bison Technical Advisory Committee, it was decided that surveys to record movements and concentrations would no longer be conducted, because sufficient information was available and decisions were made not to build corrals after all. Observations of bison concentrations continued in conjunction with calf counts and various other monitoring surveillance flights.

B. *Methods*

Between 1972 and 1975, surveys to monitor movements and concentration were usually conducted bi-monthly; between 1976 and 1979 they were generally conducted monthly. In addition to individual survey reports, annual reports were prepared that summarized the results of regular surveys (movements and concentration) and generally included information obtained from the annual total-count survey and from calf counts and anthrax surveillance surveys.

It became apparent from the large volume of data collected that a better method of recording and analyzing data was needed. Several methods of recording data on acetate overlays were tried. The results of one survey could be superimposed on the results of preceding surveys in order to illustrate movements and changes in bison concentration; this information was to be used for planning the timing of roundups.

C. *Results and Discussion*

Most of the proposed corral sites were selected on the basis of survey data obtained during 1973 (Tempany and Cooper 1975b). Of 21 potential locations, 10 were ruled out because the herding distances were too long to be practical, or because flooding was likely to occur at a time when corralling was to be carried out. From the remainder, seven areas were identified in which the concentration of bison during the effective vaccination period was high enough to warrant constructions of

corrals. These areas were Raup Lake (Site 1), Hornaday River to Darough Creek (Sites 2 and 3), Lake One (Site 4), Northarm (Sites 5 and 6), Claire River (Site 7), Revillon Coupe (Site 8), and Rosebush Creek (Sites 9, 10 and 11).

Although concentrations by zones were shown in each survey report and compared (Tempany and Cooper 1975b), it is difficult to illustrate or explain the changes in bison numbers from place to place over time. This task was made more complex by changes caused by fires, flooding, drought, differential predation pressures, and variations in winter severity. Since 1990, the wardens added a new dimension to movement studies when they began radio-tracking collared bison.

3. *Migration and Movements in Bison*

A. *Introduction*

The regular seasonal movements of bison from one range to another and back is defined as migration; it differs from local movements, which are less predictable. Information on both migratory and local movements has important implications (location of facilities, habitat manipulation, interpretive opportunities, etc.) for both the management and protection of the resource.

Little is known about the causes, timing, and routes travelled during seasonal migration and local movements. Therefore, a brief summary of the general available information can be used in further analysis and in computer-mapping the data that are already available. Future long-range plans could also usefully incorporate detailed studies of herd dynamics (movements, fidelity to specific areas) related to behavioral responses to different environments.

B. *Methods*

Information in this analysis was derived from a summary of wardens' observations. Additional impressions of migration and movements were garnered from aerial surveys, law enforcement patrols, fire patrols and ground observations.

C. *Results And Discussion*

Surveys conducted between 1971 and 1981 indicated that there were two major bison populations in the Park, one north of and one south of the Peace River, with interchange of bison between the two areas.

In addition to the two main populations a third, smaller concentration of herds is located along the Peace River (Davidson and Taerum Lakes area) along the western portion of the Park (see Figure 3). Shown in that figure are numbers associated with the different areas as determined from the 1981 surveys. Those surveys occurred in the mid range of the 20-year period and were considered accurate for that year. Flying conditions were excellent and experienced staff flew as observers, hence the conditions were ideal.

Movements across the Peace River between the main herd concentrations have been most visible in the Scow Channel area. Only a small proportion of the bison south of the Peace River are not associated with the Delta. Local movements (as opposed to migration) appeared to be generally more pronounced for bison in the Delta than for the bison north of the Peace River. It is possible that local movements may be made by any herd during any season and may in part be precipitated by wolf predation. After wolves had made kills it has been documented (see Chapter on predator/prey interactions) that herds ran as far as 86 km before settling down again. During summer, it appeared that bison responded to factors such as fire, changing water levels and, possibly, biting insects. In many cases sudden movements were observed, but no cause was apparent. Movements during winter probably occurred mostly in response to wolf predation, but also to changes in snow conditions, and food availability. A general overview of migration and movement patterns is shown in Figure 30. Radio-tracking studies will be required to refine this information.

The following general impressions are derived from the field notes made by several wardens between 1971 and 1981. North of the Peace River (Area I), bison were found during summer in small herds scattered over an area that extends roughly from the Salt Plains (mission farm area) to Peace Point and includes forested areas on both sides of the loop road. Areas of concentration have included the Salt Plains, Parson's Road, Raup Lake, Cherry Mountain, and Peace Point. Eskers, or glacier-formed ridges (visible from the air), which are extensively used during summer months, serve as travel routes from one feeding area to another. Some eskers in the vicinity of Pine Lake and McNeil Lake extend as far northwest as Flatgrass Lake and account for bison having been seen in that area during some years, although the habitat is mainly muskeg.

Where bison are found in heavily forested areas during summer, aerial surveys are not effective for identifying the important ranges, primarily because of the difficulty in finding herds in dense cover. Examples can be found in Area I where small meadows, many of which are less than one hectare in size, could be seen from the air. The Salt Plains area was of interest because it was often frequented during spring and again during fall by small herds. A few animals were also seen sporadically throughout the summer on these large ranges and open flats. During some years, bison herds have spent much of the winter on the Salt Plains (Briscoe 1978, Couchie 1978). The most recent results (1992) of summer distribution were based on radio-tracking results carried out by the Warden Service (E. Wilson, pers. comm.). In that work, four different subpopulations were identified. These are: 1) Pine Lake subpopulation, 2) Little Buffalo subpopulation extending to Grant Detour and southeast to Seton Creek, 3) Needle Lake subpopulation extending along Nylarling River as far as Highway 5, and 4) Garden River subpopulation centered on Patenaude Lake.

As temperatures cooled by September/October/November there was a general tendency for bison to move and herds were frequently seen on the loop road from Pine Lake to Hay Camp, especially between Parson's Lake and Peace Point; later

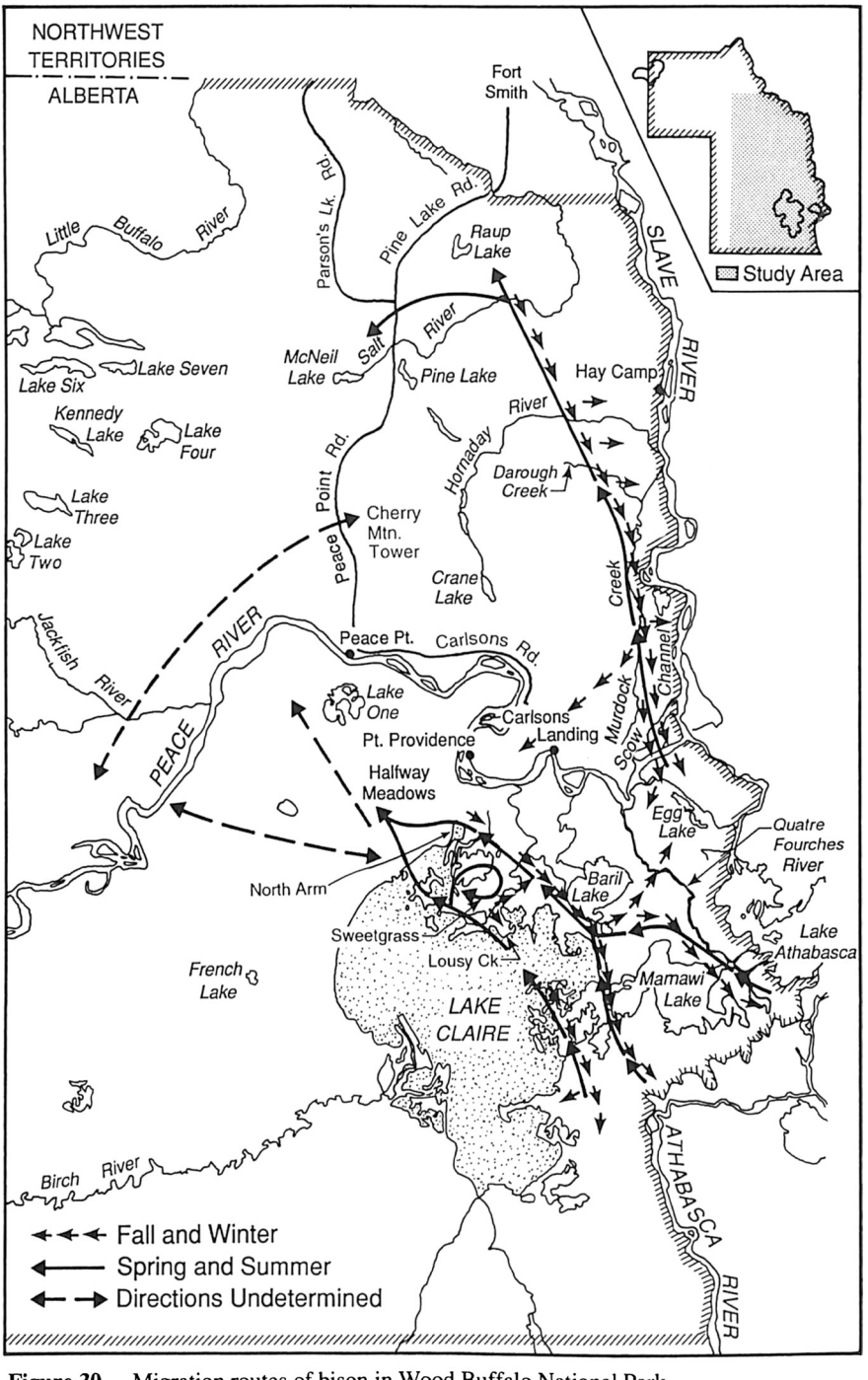


Figure 30. Migration routes of bison in Wood Buffalo National Park.

they were seen on the road between Peace Point and Carlson's Landing. Between 1971 and 1981 it appeared that there were major movements of herds or scattered individuals along a migratory trail passing Raup Lake and leading directly to the north end of Hay Camp Meadows. Bison also moved south along another route to the road between Peace Point and Carlson's Landing. It is believed that they came mainly from the summer ranges around Pine Lake, Cherry Mountain, and north of the Peace River, particularly in the area of Point Providence. By November, bison could generally be found along old river meander scars, which could be crossed once their muddy surface became frozen.

Herds that followed the Raup Lake trail gradually made their way to the meadows south of Raup Lake and in the vicinity of the south portion of the Salt River (headwaters). Some herds may have spent several days or weeks feeding in this area before moving to the Hay Camp Meadows. Other herds may have passed straight through and barely paused. The rate at which herds moved during migration appeared to be related to weather patterns. By November, there were generally several herds in the south part of Hay Camp Meadows. The exact location varied considerably from year to year, but usually extended from the corrals at the Hay Camp Station to the banks of the Hornaday River several kilometres to the west. As winter progressed and the rivers froze, there was movement onto Darough Creek Meadows. During November there were usually several herds on these ranges; they appeared to stay for several days to a few weeks. Concentrations that were amalgamations of several smaller herds sometimes occurred at this location and at Hay Camp meadows. During the early winter (November and December), there was movement eastward from the Darough Creek Meadows to sedge meadows at Murdock Creek and adjacent to the Slave River. The number that migrated to Murdock Creek Meadows seemed to vary from year to year; it also seemed that a significant proportion remained in the Hay Camp — Darough Creek Meadows area all winter. However, it was not possible to precisely quantify these movements without radio-marking animals and tracking herds over time.

When herds reached Murdock Creek Meadows they progressed southward on a route that passes through large areas of forest and a series of large meadows. A few of the meadows lie on the west side of Murdock Creek, between its numerous meanders and the Park's loop road; they were extensively used by bison. Herds were relatively easy to locate during November and December because trails left in new snow are highly visible. Although there was a general southward migration, there was some dispersal of herds on Murdock Creek Meadows.

Around the time of freeze-up on the Peace River and Slave Rivers (mid December) herds were frequently seen in the Scow Channel area. During a flight on 28 November 1963, Kuyt (1971) observed about 200 bison moving south across the river. The exchange of animals between Areas I and II has also been demonstrated by observations of an animal that was tagged at Hay Camp during 1964 and recovered along Quatre Fourches during 1971 (Kuyt 1971). Information in past reports indicates the bison cross into the Delta from Area I; observations made during the mid 1980s suggest that they seldom cross the Slave River at the northern

end of the channel. Bison appear to wait until the river ice is thick enough to cross, then make their way into the northern portion of Area II (Egg Lake area) where large, heavily-used meadows are found.

Other herds migrated to Point Providence from the direction of Peace Point; these animals probably crossed the Peace River at various points northeast of Sweetgrass Landing. The bison population on the primary ranges in Area I usually decreased by about 25% between early and midwinter, which indicates that approximately 200-400 animals migrated south across the Peace River. It is quite likely that many of these bison stay in the Egg Lake area. The actual exchange between Areas I and II needs to be studied. Populations north/south may essentially be separate units with some exchange taking place regularly; however, the degree of exchange can vary considerably depending on such factors as flooding and predator activities.

During late winter (March), when days become longer and warm weather alters snow conditions, migratory movements again became noticeable. Bison crossed the Peace River and returned north. This phenomenon was not monitored regularly enough to determine the actual size of herds and the times at which they crossed; however, fresh tracks were observed on the river when covered with snow. Movement of bison occurred northward through the Murdock Creek Meadows. By late April, several herds were usually seen on Darough Creek Meadows; herds seemed to stay there for relatively long periods and grazed over the entire area. Whereas the Hay Camp Meadows area is usually very wet after most of the snow has melted, Darough Creek Meadows is at a slightly higher elevation than the surrounding land and thus may be drier. In addition, Darough Creek Meadows are believed to have been the most important calving area in Area I. These two factors may partially explain why herds remained for a long time in the Darough Creek Meadows before moving northward toward summer ranges. By the end of May, most herds had moved north to Raup Lake and west onto summer ranges. By June it was increasingly difficult to locate herds as they dispersed into forested areas. Raup Lake was believed to be an important calving range during the early portion of the study period. There may have been a shift in preference to other areas by the late 1970s and early 1980s.

As extensive melting of snow occurred, herds that had migrated to the winter ranges in the Point Providence area began to leave for summer range. Herds were observed along Carlson's Road during April. During May and June they dispersed in a northwesterly direction into forested areas. Although the area south of Pine Lake is mainly forested, foraging did occur in the understorey along the numerous trails that interconnect the feeding areas that are probably preferred by bison. Some observers have seen herds within previously burned areas taking advantage of new growth. Fuller (pers. comm.) did not see this occurring in the 1950s and 1960s.

In Area II, the major summer ranges were in the Sweetgrass area. Because parts of this area are at a higher elevation than other parts of the Delta, in most years it is not affected by flooding. During the summer in which flooding occurred at Sweetgrass Meadows (1974) large numbers of bison moved to higher ground at

Halfway Meadows and to Lake One, or they used the dry *Carex* and *Calamagrostis* meadows that extend into the Delta on the north side of Lake Claire. The Lousy Creek area was important calving range when the 1985 to 1991 observations were carried out.

By September/October there was already movement, first eastward and then southward, toward winter ranges. As streams, rivers, sloughs, and lake shores in this region freeze, vast sedge meadows become accessible to the bison that have spent the summer west of Baril Lake. One migratory route passes north of Baril Lake, then northeast across the Chenal des Quatres Fourches to meadows in a somewhat more southerly portion of the Delta. Another route passes around Baril Lake, then southeast around the north end of Mamawi Lake. A route south of Baril Lake takes bison southward to Prairie Creek, Hilda Lake, and Welstead Lake, and across to the Birch River Delta. A considerable amount of dispersal and foraging occurred along the way on all routes; in some cases it took most of the winter before herds used the remote parts of their range. Bison foraged in an area for several days to a few weeks then moved to another zone — the reasons for movement were not always obvious. During many years bison migrated to ranges outside the Park, especially in the vicinity of Galoot Lake, and were heavily hunted by local natives from Fort Chipewyan, Alberta.

From one winter to the next, there were frequent shifts in concentration between zones. These movements may have been influenced by changes in water levels, forage availability, the effects of fire, etc. Similarly bison will shift their movement within a winter. For example, freezing rain could affect one zone more than another, causing bison to move to meadows where snow crust was not a major hinderance to feeding.

During late March, when mild temperatures began to affect snow and ice conditions, there was gradual (or sometimes major) movement back toward the summer range west of Baril Lake.

It is believed that most calving in Area II took place in the Sweetgrass area and south of Sweetgrass along Lousy Creek during May and June. During the summer there was some movement of bison to Lake One Meadows and the west shore of Lake Claire, where suitable sedge meadows were found. The use of Lake One was variable, and was probably affected mainly by conditions in both the Delta and at Lake One. Huge summer herds (numbers exceeding 1,000 animals) were seen at Lake One in the late 1970s. This could have been partly a result of the post 1974 flooding conditions. Large herds were not seen at Lake One during the summers of 1980, 1981 and subsequently. A remarkable infestation of grasshoppers that could have affected the range was noted at this location in 1981. A. Simpson (pers. comm.) saw one herd of about 50 cows and calves winter at Lake One in 1989. Simpson also noted that at one time the Lake One area contained "islands" (peninsulas) on which cows were seen with their calves. In his experience, major lakes existed in the area from about 1932 to 1949. At that time also, a number of natives and white trappers lived in the area.

4. *Anthrax Surveillance*

A. *Introduction*

Anthrax patrols began immediately after the presence of the disease was discovered in the Park area in 1964. In order to determine the severity of the problem and to dispose of the cadavers, aerial surveys were conducted. During the surveys, information was also gained on the distribution of bison on their summer ranges.

B. *Methods*

Between 1965 and 1971, air patrols in the northern areas outside of Wood Buffalo National Park (Grand Detour, Hook Lake and Brule Point, N.W.T.) were conducted once a week, beginning in early April. Other areas were occasionally covered by surveillance patrols. Frequent reconnaissance of all major primary ranges began on approximately 15 June; the frequency was gradually reduced throughout the summer, and the patrols were concluded by the end of August.

Between 1971 and 1982, anthrax surveillance flights usually extended into September. The schedule of flights was adjusted according to weather patterns. It was believed that an outbreak of anthrax was most likely to occur under hot weather conditions when the mean temperature was above 16°C, especially following a rainy period (Tempany and Cooper 1974). It was originally intended that flights would be scheduled for at least once every three days during warm, clear weather. However, due to other commitments, the schedule was rarely carried out exactly as planned.

Total-count and migration surveys were conducted separately from anthrax surveillance surveys, even though the same ranges were covered. The anthrax surveillance flights had a single purpose — to locate carcasses — so little time was spent counting bison. The search pattern had to be variable in order to properly cover forest edges and the margins of lakes, streams, and rivers. For the purposes of anthrax surveillance, three general zones were delineated. The northern zone included the region west of the Little Buffalo River, the Foxhole area, and the area west of the loop road (all inside the Park), as well as the Grand Detour area (outside the Park), while the mid-zone included the area within the loop road, and the McNeil Lake, Murdock Creek, Point Providence, and Salt Plains areas (all inside the Park). The southern zone consisted of all of Area II (south of the Peace River), as well as the Davidson Lake and Burrison Lake areas north of the river (Tempany and Cooper 1974).

A generalized flight pattern was drawn up during 1976 (prior to that the flight pattern had been quite random); however, a consistent pattern was rarely flown, except perhaps along the Little Buffalo River in the northern part of the Park. Although the principal objective was to conduct searches over the main bison ranges, the actual flight path was usually dictated by the preferences of each navigator and thus could vary considerably. The areas searched included open prairies, aspen parkland intermixed with prairies, forest edges and clearings, stream

edges, and lake shores. Searches were conducted in areas in which bison had recently been seen; information from recent surveys was also used in assessing the areas in which surveillance was desirable.

The areas of primary range covered most often were the meadows around Raup Lake, Salt Plains, Hay Camp, McNeil Lake, Lake One, Murdock Creek, Point Providence, the Peace-Athabasca Delta, and the Little Buffalo River. Little time was spent covering secondary ranges. A map was available that defined summer ranges (and thus areas of concentration) in Areas I and II (Tempany and Cooper 1975b). The amount of time spent in search of carcasses in a given area was not always correlated with previous bison distribution.

Aircraft capable of slow speeds were the most useful. Fixed-wing aircraft such as the Cessna 172, Cessna 180, and Cessna 185 were preferred because their high wing position allows excellent visibility. Helicopters were used several times during 1973, but proved to be too costly and noisy.

Searches were made from altitudes of 240-360 m and at speeds of 128-224 km/hr; both criteria could vary, depending on local conditions (Tempany and Cooper 1974). Binoculars, cameras, and tape recorders may have been used, but are not mentioned in any of the survey reports. Most of the survey reports do not mention how data were recorded, or what kind of maps were used. It is believed that topographic sheets with a scale of 1:250,000 were generally used by navigators to record data during flights. These original survey maps probably indicated bison distribution and herd sizes. Tempany and Cooper (1974) recorded data by using a system of gridded maps with plastic overlays. Unfortunately, those records are no longer on file. Apparently there was no consistent policy for filing and storing results. Maps are available for most flights carried out between 1980 and 1982 in Area I.

After 1979, the timing and some of the methods used during surveys changed. Migration surveys were no longer carried out during the summer, and some anthrax surveillance flights were carried out in conjunction with regular fire patrols conducted by Parks Fire Control operations. During 1980, the area from Garden Creek north to Burrison Lake was thoroughly covered after two carcasses were discovered there (Park files 1980).

In the past there has been considerable difficulty in locating bison on summer ranges in Area I because they commonly inhabit forested areas and previously burned areas. More effort was expended during the 1980s to locate the small prairies and sloughs within forested areas that bison regularly visit. The most recent anthrax outbreak occurred in the summer of 1991.

C. *Results and Discussion*

Table 17 lists the number of carcasses that were located during anthrax surveillance flights. These flights were not carried out in a consistent manner. Insufficient data were recorded in reports or on maps to provide any detailed information on calf

Table 17. Bison deaths attributed to anthrax in Wood Buffalo National Park and the Northwest Territories, 1962-1991 (Millette and Sturko 1977, Park Warden and Northwest Territories Wildlife Service files, and S.V. Tessaro, pers. comm.). No deaths were attributed to anthrax between 1979 and 1981. No surveys were done during missing years; only since 1978 were accurate locations plotted. The latest outbreak occurred in 1991.

Location	1962	1963	1964	1965	1967	1968	1971	1978	1991	Total
WOOD BUFFALO NATIONAL PARK:										
Lake One/Lake Claire/French Lake	-	-	7	111	120	1	-	3	-	242
Sweetgrass	-	-	-	-	-	-	-	1	-	1
Hay Camp	-	-	46	-	-	-	-	2	-	48
Raup Lake	-	-	-	-	-	-	-	19	3	22
Raup Plains	-	-	-	-	-	-	-	12	-	12
McNeil Lake	-	-	-	-	-	-	-	4	8	12
Klewi River	-	-	-	-	-	-	-	3	-	3
Canso Meadows	-	-	-	-	-	-	-	2	-	2
Nyarling River	-	-	-	-	-	-	-	1	-	1
Parsons Lake	-	-	-	-	-	-	-	1	13	14
Salt Plains	-	-	-	-	-	-	-	-	6	6
Cherry Mountain	-	-	-	-	-	-	-	-	1	1
Total	**-**	**-**	**53**	**111**	**120**	**1**	**-**	**48**	**32**[1]	**365**
NORTHWEST TERRITORIES (outside park)										
Hook Lake	281	12	44	-	-	-	31	13	-	381
Grand Detour	-	269	202	-	-	-	-	-	-	471
Little Buffalo River	-	-	-	-	-	-	-	26	-	26
Total	**281**	**281**	**246**	**-**	**-**	**-**	**31**	**39**	**-**	**878**

[1] Five bison out of 52 radio-collared died from the anthrax outbreak in the area north of the Peace River. Wardens estimated that about 250 bison died of anthrax in Area I in the summer of 1991.

counts, distribution during summer, or movements. A total of 365 anthrax-infected carcasses were found during surveillance flights.

In the latest outbreak, 1991, five of 44 collared bison north of the Peace River died of anthrax. None of the eight bison collared south of the river died from anthrax. One animal collared at Lake One on 23 July was found dead on 10 August in the Salt Plains area (Wilson, pers. comm.). Anthrax outbreaks occur during the peak rutting period, rendering bulls susceptible because of widespread movements. Wardens estimated that about 250 animals may have died of anthrax in 1991.

5. *Herd-Size Dynamics*

A. *Introduction*

Bison spend most of their time in mixed-gender groups (McHugh 1958). Mixed herds vary in size and consist of cows, calves, yearlings, and sometimes, older bulls. Bulls also form small herds (5-15) or occur as solitary animals. The degree of stability in the composition of mixed herds is still unknown, but observations in the Park have clearly shown the fluidity of herd size dynamics.

Little is known about home ranges of bison in Wood Buffalo National Park, although studies are now in progress (Van Camp et al. 1991, Wilson and Milne 1992). Studies in the Mackenzie Bison Sanctuary indicated that the areas used by individual bison ranged from 179 km^2 to 1,442 km^2 (Larter and Gates 1990). Home ranges of bulls were smaller than those of cows (433 km^2 as compared to 897 km^2 for cows). The dynamics of herd leadership are not clear for bison. Like the gaur (*Bos gaurus gaurus*) (Ullrich 1968, cited by Sinclair 1977) and the water buffalo (*Bubalus bubalus*) (Tulloch 1967, cited by Sinclair 1977), but unlike another social bovid, the muskox (*Ovibos moschatus*) (Gunn 1982), mixed-gender bison groups generally appear to be led by cows. Research on domestic cattle (Schein and Fohrman 1955) suggests that age — i.e., "seniority" — is of primary importance in determining rank. The social position of same-aged animals is apparently established at three to six months of age and manifests itself as the animals become older. McHugh (1958) believed that leadership was not exclusive in a confined bison herd. Details are not available for free-roaming bison. In the latter, contagious behaviour, that is, movement in the same direction at the same rate, appears to be common. According to Reynolds et al. (1982) it is not clear whether matriarchal groups exist, and if they do, whether the members are consanguineous. Seton (1929) and Soper (1941) suggested that herds are consanguineous, but did not present specific evidence. On the other hand, Garretson (1938), McHugh (1958), Fuller (1960), Van Vuren (1983), and Lott and Minta (1983) believed that herd composition is fluid and changes frequently (i.e., that bison herds are not consanguineous).

Considerable variation has been reported in the literature on the average size of bison herds. Herds ranged in size from 19-480 in Yellowstone National Park (McHugh 1958) and from 11-30 [11-20 (Fuller 1960), 11-30 (Egerton 1962)] in

Wood Buffalo National Park. Fuller (1960) believed that both mixed herds and bull herds are smaller in forested areas than in open areas. Because different methods (ground versus aerial observations) were used within and between parks, the results are not directly comparable. If anything, groups of bison in forests probably more accurately represent typical social units (mixed herds or small bull herds), whereas groups of bison in meadows are "aggregations" of herds and/or parts of herds.

The herd-size dynamics of the bison in Wood Buffalo National Park are probably influenced by environmental factors. The presence of suitable range, particularly during winter, will attract bison, which can be seen in large aggregations that can reach up to 1,000 or more animals. Cold winter weather with high windchills may also cause bison to seek shelter in forested areas. Depending on the availability of forest cover, this may result in large groups forming smaller units or vice versa. Reynolds et al. (1978) observed that during winter, bison on the Slave River Lowlands foraged in small sheltered meadows, which would tend to divide herds. During migration bison travel along specific trails that connect winter and summer ranges; thus herds tend to be drawn together at the times when movements are greatest.

Seasonal diet and habitat selection undoubtedly influences movements (Melton et al. 1989). Because of different environments north and south of the river, some differences of habitat dispersion likely is reflected in food selection. Studies in the Mackenzie Bison Sanctuary showed pronounced seasonal changes in diet. Sedges (mostly *Carex antherodes*) provided in excess of 95% to the winter diet (Larter and Gates 1991). Summer diets are more diverse including sedges, grasses, willow and lichens. The lichen *Cladina mitis* became a major source of food in the fall. The fall period in the sanctuary was marked by a less distinct habitat preference and greater use of forested areas. Wet sedge meadows were selected in winter and provided the most readily available source of crude protein (Larter and Gates 1991).

The peak of spring migration probably occurs during March, prior to calving. Calef and Van Camp (1987) reported that bison on the Slave River Lowlands are concentrated in large meadows during the calving and post-calving periods (May to June). The largest social units found during the year are formed during the post-calving period. It is possible that, because the greatest exposure to wind occurs on open terrain, some relief from biting insects may be gained there, further increasing the tendency to aggregate in open areas. Some wardens in Wood Buffalo National Park have speculated that during the height of the insect season (midsummer), bison in the region north of the Peace River retreat to wooded areas (D. Anions, field notes).

Kelsall (1968) has suggested that in other species (e.g., caribou), aggregations of herds formed during the post-calving period are an antipredator mechanism. The relationship between herd size and predation is not clear for bison, but it has been speculated that the grouping of young calves into pods is a behaviourial antipredator response (Carbyn and Trottier 1987).

When not seriously affected by external factors and if social influences are unimportant, the size of bison groups could be expected to remain stable for most

of the year. However, this is not the case. Calef and Van Camp (1987) found that the mean size of bull groups in the Slave River Lowlands reached a maximum of 4.2 during the post-calving period and decreased to 1.3 during the rut. As bulls joined mixed groups at the onset of the rut, the herds formed during the post-calving period tended to break up. The average herd size continued to decrease until early winter, when herds aggregated on wintering ranges (and herd size increased). The above observations, all of which were made in the Slave River Lowlands, provide a suitable example with which to compare the trends observed in Wood Buffalo National Park.

Allison (1972) saw herds and aggregations of herds of up to 600 animals on the Peace-Athabasca Delta during the early 1970s. These sightings were confirmed by subsequent wardens' observations. From general observations, Allison further stated that average herd size declines during the rut (no mention of post-calving-period aggregations), followed by an increase in the average size of groups during early winter. During midwinter, the size of the herds observed on the Peace-Athabasca Delta decreased as bison increasingly used forested portions adjacent to the Delta. According to Allison (1972), regrouping occurred with the onset of warmer weather in March.

The effect of different snow depths on herd size has not been studied. Greater access to food may be provided when groups form craters than when individuals attempt to forage by themselves. Fuller (1950) recorded a single herd of 729 animals on the Delta (between Baril Lake and the Northwest arm of Lake Claire) during winter. A check of wardens' data indicated that herds exceeding 700 animals were reported during winter at least five times between 1971 and 1981 (see Results below). A herd seen at Lake One in August 1978 exceeded 800 animals. Snow conditions along protected watercourses may be more favourable for winter foraging than conditions in large, windswept areas. If this is the case then deep snow, particularly during late winter, would have the effect of dispersing bison. It is doubtful that the data obtained from general surveys would provide sufficient detail to allow subtle variations in herd-size structure to be clarified. Nevertheless, the data was analyzed to determine whether any trends were discernible.

B. *Methods*

The herd-size information obtained from aerial surveys conducted between 1970/71 and 1981/82 was plotted on maps. The results were examined, but in some cases it appeared that the data had not been accurately plotted; in such cases, the information was not used. The criteria used in deciding which information to include was the location of the information plotted in relation to known ranges and the size of the circles drawn around each number (indicates the accuracy with which the data were plotted). For example, a number with a large circle in a known extensive open area would indicate little effort was made to designate accurate herd size information. The data was grouped into several periods: 1 April - 15 June (calving period), 16 June - 31 July (post-calving period), 1 August - 30 September

(rutting period), 1 October - 30 November (post-rutting/early winter period), 1 December - 31 January (midwinter), and 1 February - 31 March (late winter). These designations were made on the basis of observations made in the field, and on data collected while conducting surveys.

C. *Results And Discussion*

The information on seasonal changes in herd size between 1970/71 and 1981/82 is summarized in Table 18. The changes in herd-size dynamics are illustrated in Figure 31.

The average herd size was similar to that found by Egerton (1962) and slightly higher than that determined by Fuller (1960). The results obtained during aerial surveys may be slightly inflated by the tendency of observers to concentrate on aggregations in open areas.

Wardens' records show that aggregations exceeded 700 animals on at least five different occasions. Two of these observations were made shortly after the spring floods during 1974, and undoubtedly reflect the fact that the amount of available range was reduced. The dates, numbers, and locations were as follows:

28 February 1973 — 1,676 bison at the Baril River, northwest of Baril Lake;
3 April 1974 — 990 bison west of the Claire River-Sweetgrass area;
15 July 1974 — 1,000 bison (exact location not available);
23 December 1974 — 750 bison west of the Lake Claire-Sweetgrass area; and
19 June 1981 — 1,000 bison (exact location not available).

During all years between 1970/71 and 1981/82, the mean herd size was observed to increase between the calving and post-calving periods (Figure 31). In this instance observations matched predictions. This was not the case for the post-calving and rutting periods. In three of the eight years for which data were available, mean herd size either increased or decreased only slightly, and in two of the years, mean herd size did not change, suggesting that the size of post-calving and rutting herds is essentially the same. Similarly, there was no indication of significant changes in herd size between the rutting period and the post-rutting/early winter period, nor were mid and late winter herds significantly different in size. More refined studies (e.g., radiotelemetry and long-term monitoring) would be required to accurately monitor herd size (and composition). The average size of herds decreased as the population declined from 1971 to 1991 (Table 19). This information was obtained from Peterson (1991), who summarized mean herd size recorded over the years. Trends were important and the data set defined the changes over time (Table 19). As expected, average herd sizes had declined with the decline of the population. Largest herd sighted in each survey were between 200 and 400 from 1974 to 1988. Numbers dropped below 200 after 1989.

Herd-size data were not well documented during early wardens' surveys (1971-1980). In some cases, accurate counts were recorded in field notes, but were

Table 18. Summary of annual herd-size dynamics, as determined from data collected during aerial surveys, 1970/71 to 1981/82. Data were not used where herd-size information appeared to have been recorded inaccurately.

	Spring - Summer									Fall - Winter								
	1 Apr - 15 Jun			16 Jun - 31 Jul			1 Aug - 30 Sep			1 Oct - 30 Nov			1 Dec - 31 Jan			1 Feb - 31 Mar		
	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n
1970/71	-	-	-	-	-	-	-	-	-	-	-	-	43.94	-	351	34.36	1.5	1006
1971/72	-	-	-	-	-	-	-	-	-	46.15	3.9	100	30.07	0.9	1057	37.16	1.7	722
1972/73	25.92	1.8	370	63.73	19.3	11	47.28*	3.5	99	40.80	2.6	484	37.22	1.8	744	31.64	2.6	1025
1973/74	28.40	1.7	850	78.82	9.0	68	-	-	-	32.06	2.2	424	28.07	1.5	693	27.49	1.6	1008
1974/75	22.38	1.6	1026	31.95	4.1	142	16.42	2.8	155	28.03	5.0	114	26.88	2.5	568	19.46	1.3	801
1975/76	18.69	1.2	839	47.40	5.1	184	20.67	1.9	303	21.58	1.9	314	21.12	1.5	429	14.4	0.9	789
1976/77	31.78	2.9	326	35.40	4.5	174	21.71	1.9	266	19.66	1.6	425	21.50	1.6	600	16.61	1.2	805
1977/78	22.80	1.9	475	29.33	5.5	93	19.95	2.8	202	18.46	1.6	384	17.39	1.9	415	15.36	1.3	557
1978/79	16.20	1.3	469	29.82	3.6	175	18.84	2.6	180	21.01	2.6	144	18.01	1.5	481	21.97	2.3	204
1979/80	-	-	-	-	-	-	30.14	5.7	44	21.03	1.8	226	21.54	2.9	182	6.14*	0.9	105
1980/81	21.30	7.7	10	182.00*	48.0	2	19.80	2.3	69	23.03	4.9	35	18.30	5.7	30	14.94	1.8	405
1981/82	12.81	2.9	54	35.94	16.2	63	23.74	3.4	85	20.40	5.5	55	-	-	-	-	-	-
$\bar{X}$	22.25			59.38			24.28			26.56			25.82			21.78		

*Indicates anomalies.

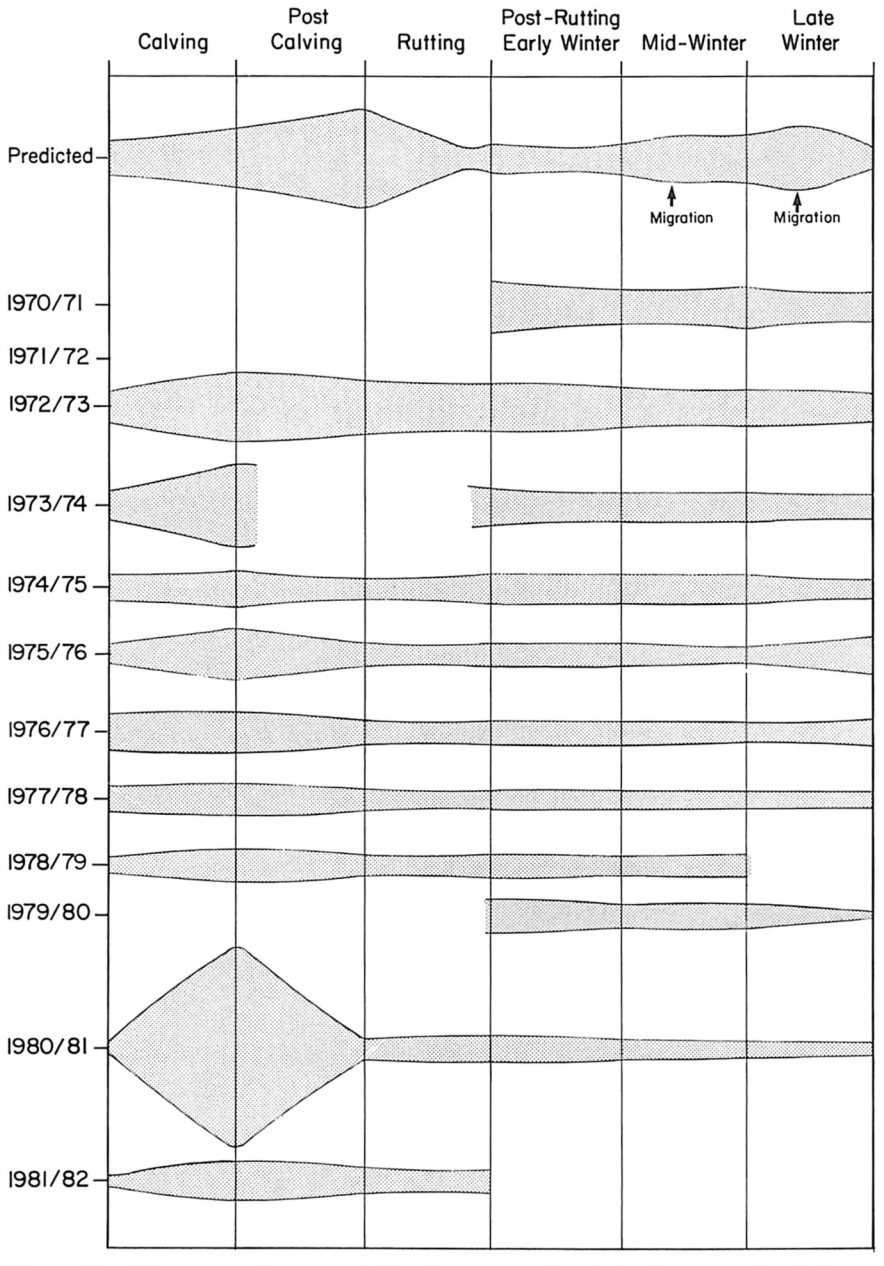


Figure 31. Diagrammatic representation, by season, of variation in average herd-size dynamics in Wood Buffalo National Park, as determined from wardens' surveys, 1970-1982.

Table 19. Mean bison herd size recorded during total count surveys conducted in February and March from 1974 to 1991, Wood Buffalo National Park. Data for 1978, 1982 and 1986 were excluded.

Year	# Of Herds	Mean	S.D.	S.E.	Max. Herd Size	Total Bison In Herds (that Were Recorded)	Total Count
1974	197	37.37	48.46	3.45	405	7362	8401
1975	190	26.77	36.26	2.63	215	5086	5527
1976	191	25.59	33.48	2.42	298	4887	6061
1977	159	30.53	39.25	3.11	200	4854	5170
1979	169	28.34	31.91	2.45	215	4789	5539
1980	132	31.72	42.53	3.70	240	4187	4521
1981	157	29.22	45.96	3.67	284	4588	5558
1983	166	29.37	43.97	3.41	276	4875	5006
1984	132	31.30	55.44	4.83	476	4132	4667
1985	147	28.67	49.38	4.07	434	4214	4582
1987	155	22.87	36.16	2.90	228	3544	4139
1988	145	25.06	41.22	3.42	297	3634	4130
1989	144	20.40	29.15	2.43	140	2937	3254
1990	147	18.23	20.40	1.68	115	2680	3375
1991	151	17.01	21.40	1.74	186	2568	3310

NOTE: errors in data from 1978, 1982; no data for 1986.

not mapped. More emphasis was placed on accurate recording and mapping between 1981 and 1983. A number of investigators have discussed average herd size (Fuller 1960, Egerton 1962, McCourt 1970, Kuyt 1971); McCourt (pers. comm., cited by Allison 1972) noted that the results recorded by different investigators may not be comparable because different criteria might have been used to define the herds. This also applies to survey data collected by wardens, particularly because many different individuals were involved in gathering it. In the future, more effort should be directed at quantifying the sizes of herds. Such information can be useful when examining the relationship between range preference and population density.

6. *Calf Surveys*

A. *Introduction*

Fecundity is a measure of output per reproductive unit (i.e., mature females). Since bison are polygamous, under normal circumstances there should be an adequate number of bulls to breed with all mature females, so a female-biased sex ratio should theoretically not influence productivity. However, if enough bulls were rendered sterile by disease, the sex ratio of mature bison could become biased to the point that productivity would be affected. Brucellosis is a disease that causes abortion in bovids, therefore, the incidence within the population of Wood Buffalo National Park could be affecting calf production. The reproductive vigour of female bison is highest between the ages of 3 and 13 years (Shaw and Carter 1989) although much older cows are known to have produced calves regularly (H. Reynolds, pers. comm.). Fuller (1961) reported that one out of 11 yearlings examined was pregnant, resulting in few births for two-year-old animals (8 of 177). Fuller (1966) later showed that in a sample of 733 cows (2 years or older) examined at Hay Camp, 26% did not show any sign of reproductive activity (i.e., pregnancy, lactation, or both). This figure was 15% for Delta herds. Fuller (1966) also noted that the proportion of bison calves in Area I was lower than that in Area II, although not significantly so (chi-square test; $p > 0.05$), and suggested that this may be because, at the time, females in Area II produced young at an earlier age than did those in Area I. Halloran (1968) found that 73% of female plains bison studied in Oklahoma had their first calves at three years of age or older. Fuller (1966) believed that mature cows produce an average of two calves every three years. If no calves die at birth, the number that could be expected is about 67 calves/100 cows. Data on pregnancy rate (Table 20) indicates average rates of 62% (including 2-year-olds) and 38% for older cows. Overall pregnancy rates were recorded at an average of 47%.

The sex ratio of bison at birth is approximately equal (Shaw and Carter 1989), although males are favoured *in utero* (Rush 1932, cited by Meagher 1973; Fuller 1966, Halloran 1968). When the data for this monograph was analyzed, it was assumed that age and sex ratios do not change over time, and thus that the proportions of pre-reproductive and reproductive females did not vary during the study period. This assumption is probably not valid, but in the absence of conclusive data, it had to be made so that the results from year to year could be compared. The proportion of pre-reproductive females probably fluctuates significantly, depending in part on the number of calves produced the previous year and on the rate of survival to one year of age. It is often assumed that annual changes in calf/cow ratios reflect a change in the abundance of offspring produced, but this assumption does not take into account changes in the number of both reproductive (cows) and non-reproductive components (bulls, yearlings). The reproductive output of a population probably also varies with the longevity and physiological condition of older animals. As with the number of bison that survive to reproductive age, the number that survive to post-reproductive age can be expected to change with

Table 20. Pregnancy rates by age class and location of bison in Wood Buffalo National Park, based on slaughter data[1] (average pregnancy rate of 47%).

		2-Year-Old		3-Year-Old		4-Year-Old		Young Adult* >4-year-old		Adult*		Aged*		Total		
			%		%		%		%		%		%		%	
Year	Location	N	Pregn.	N	Pregn.	N	Pregn.	N	Pregn.	N	Pregn.	N	Pregn.	N	Pregn.	Reference
1952	Lk. Claire	17	58.8	31	80.7	-	-	42	85.7	9	77.8	6	33.3	105	66.7	Fuller1962
1952-56	Hay Camp	160	38.1	92	65.2	120	62.5	95	66.3	192	58.3	74	25.7	733	53.2	Fuller 1962
1957	Sweetgrass	39	28.2	34	50.0	25	72.0	33	69.7	45	62.2	17	52.9	193	54.9	Olson 1958
1958	Sweetgrass	31	64.5	35	74.3	26	80.8	17	76.5	19	57.9	5	60.0	133	70.7	Novakowski 1958
1959	Sweetgrass	37	27.0	40	32.5	24	45.8	36	58.3	69	47.8	9	22.2	215	41.9	Choquette & Stewart 1959
1961	Sweetgrass	18	5.6	38	36.8	29	31.0	32	46.9	21	33.3	10	10.0	148	31.8	Novakowski & Choquette 1961
1963	Hay Camp	2	50.0	14	28.6	4	50.0	17	58.8	18	27.8	2	100.0	57	42.1	Novakowski & Choquette 1963
1964	Hay Camp	12	33.3	16	56.3	16	68.8	52	30.8	4	0.0	4	0.0	104	38.5	Novakowski & Choquette 1964
1974	Sweetgrass	1	0.0	3	0.0	2	0.0	-	-	55	23.6	-	-	61	21.3	Broughton 1974

*Precise definition of this class was not stated.

[1] Published with permission, University of Saskatchewan, Tessaro 1987.

changing environmental conditions. Fuller (1966) noted that reproductive activity of old cows is reduced. However, he also did mention that one cow that was killed in Wainwright was of the original Pablo herd and was pregnant at age 39 years.

Bulls exhibit sexual maturity at a later age than cows. A small percentage (10-20%) of yearling bulls sporadically shows signs of spermatogenesis, as indicated by the presence of sperm in the epididymis (Fuller 1966), but these animals probably do not breed because of the dominance of older animals (McHugh 1958, Fuller 1960, Meagher 1973).

Female bison are polyestrous, with an estrous cycle of about three weeks (Fuller 1966); their gestation period is about 285 days (Halloran 1968). Haugen (1974) back-dated the time of conception for bison in Nebraska and South Dakota from the size of embryos and concluded that the rutting period extended from July to September, with two peaks in activity. The first peak occurred between 21 July and mid August, while a second but smaller peak occurred between 25 August and 3 September. The second peak probably corresponds with a second estrous cycle; if bison are similar to cattle, females can be expected to come into a second estrous 17-24 days after the first (Haugen 1974). In Wood Buffalo National Park, serious mating activity begins in early July. According to Fuller (1966), the peak is reached from 10-20 August. Field observations in 1989 and 1990 revealed considerable rutting behaviour still displayed in early October. Haugen (1974) speculated that females in their first estrous cycle have less chance of being bred than do older cows. One could thus expect two peaks in calving during spring and different sized embryos during winter kills. A further influence on the timing of an individual's estrous cycle may be the presence of a nursing calf. In domestic cattle, cows with nursing calves have a longer period between calving and the onset of estrous than do those that are not nursing. Fuller (1961) found that lactating cows in Wood Buffalo National Park carried smaller fetuses than nonlactating cows, which may suggest that cows with calves breed later than do dry cows. Bison cows with suckling calves probably come into estrous late, but still within the rutting period, or may come into estrous past the peak of the rut. In addition, there may be other complicating factors such as disease or nutrition. In fact, conception, and hence calving, can occur at any time; newborn calves have been seen during every month of the year in Wood Buffalo National Park. The regular calving season starts as early as April, but calving probably peaks during late May and early June. Some cows are still visibly pregnant in mid June (L. Carbyn, field observation). This conclusion was reached by watching herds and noting the appearance of the cows from close quarters.

Calves are readily distinguished in the herd from the time of birth until approximately one year of age. Until their first moult (at 3 months of age, Meagher 1978) calves are light brown in colour, after which their colour becomes darker. Between three and thirteen months of age, calves can be readily distinguished from adults by their smaller size. Thereafter, "long-yearlings", and "short two-year-olds" appear similar and cannot always be distinguished from one another. Wardens have classified calves during aerial surveys. Comparing the size of calves and yearlings

from the air has been possible (Tempany 1976), but this causes disturbance. The accuracy of these methods is still in question and was never tested. Ground counts have successfully replaced aerial calf counts since 1985.

The timing of aerial calf surveys varied considerably between 1971 and 1981, partly because there was no ideal time to conduct them. Initially they were carried out more frequently during June, but subsequent surveys were more often conducted during August. As noted above, calving may not be complete at the time of the surveys during June, so calves born later than this would not be recorded. Furthermore, some calves born after June may die as summer progresses; these animals would not be counted during surveys conducted in late summer (August). Some aerial surveys were conducted during October to determine calf survival over the first four months; further surveys took place in March to account for winter losses. Logistically, surveys conducted during October and November were easiest because at this time, bison congregate in large herds, move to wintering grounds, and are more visible, especially after the first snowfall. The timing of surveys also varied with different observers. Unless individual herds are closely studied, the problems encountered in making accurate calf counts and estimates of mortality cannot be overcome.

Calving areas are located both north and south of the Peace River, and because of forest cover, it was difficult to classify cow/calf herd composition in Area I. Because environmental conditions (e.g., winter severity) and biological factors (e.g., wolf predation) vary between locations, an attempt was made to separately evaluate the wardens' data collected on aerial surveys from the north and south regions.

The objectives of this analysis were as follows:

1. To compare the percentage of calves in Area I and Area II during the same years.
2. To compare the total percentage of calves between years.
3. To determine the precision of calf-count surveys by conducting several surveys of an area between June and August of the same year, and comparing the results. Significant differences within a year would suggest either that calf proportions vary during the summer or that the surveys themselves were not precise.
4. To examine the relationship between the duration of the periods of critical snow depth for cows (>65 cm) in a given year and the percentage of calves born during the following summer in both Area I and Area II.
5. To determine the sample sizes required to produce 95% confidence limits for the estimates of calf production.

B. *Methods*

The aircraft used were generally the same as those used for the total-count surveys. There were usually three observers per flight — the navigator sat in the front seat, directed the pilot, recorded data on a map, and occasionally took photographs; the second observer was seated behind the pilot and recorded sightings and other information; and the third observer, seated behind the navigator, was responsible for counts and usually took photographs. Different approaches were used when there were only two wardens available — the navigator recorded data and usually took photographs, and the second observer, who was seated behind the navigator, recorded information and also took photographs.

The altitudes from which calf surveys were conducted varied little over the years. Some of the variation between flights resulted from differences in habitat, snow conditions, and the size of herds. Since 1975, aerial surveys have usually been carried out at altitudes of approximately 300 m agl (Tempany 1976) because the disturbance factor is too great at lower altitudes.

Photographs were taken to identify the number of calves in larger herds. These were usually taken at altitudes of approximately 180 m agl, in spite of the disturbance factor, but there has been some variability depending on the size, spread, and behaviour of the herd, and on the amount of forest cover. A variety of cameras, lenses, and films have been used. At the beginning of calf-count surveys, McCourt (1970) and Allison (1972) used Hasselblad cameras mounted in a Piper Apache aircraft. The equipment used by wardens was discussed by Stelfox and Tempany (1976). Large herds confined to a relatively small area are hard to photograph, therefore an automatic film-advance system was used. A Nikon F-1 or F-2 camera and a 135-mm lens were used in both Areas I and II, but the motor drive was not always used in Area I. Smaller herds seldom required more than two photographs per herd. Wide-angle lenses (e.g., 43-85 mm and 55 mm) were also used to encompass large or widely scattered herds in one photograph. A Pentax 35 mm camera with a 135-mm telephoto lens was occasionally used in Area I.

During 1976, Stelfox and Tempany outlined a procedure for taking photographs, which was basically followed until 1981 (Anions and Fremont 1981). The pilot was instructed by the navigator to approach the herd from a specific direction, reduce the altitude to 180 m agl, and reduce the flying speed to 120 km/hr. Photographs were taken at an angle of roughly 45° to the aircraft. The best results were obtained when the pilot flew into the wind while reducing airspeed, for a long, steady approach. If necessary, the aircraft could be tilted slightly toward the herd while passing, which produces a better angle for photography. Photographs were analyzed from either prints or slides.

Calf ratios were also determined during vaccination roundups. Reports are available for 1970, 1972, 1973, and 1975. Calf percentages were compared between years using contingency tables, and pairwise comparisons were used to identify the possible sources of outside influences (e.g., flooding, winter conditions). If more than one calf count was available then the largest number was used, because it was

assumed to be the most representative. The relationship between the duration of the period of critical snow depth in a given winter and the percentage of calves born during the following summer was examined, using linear regression.

Confidence intervals were determined by the method of Czaplewski et al. (1983). The levels of precision for the data on calf counts conducted in Areas I and II from 1970-1981 were grouped by time period. The calf-ratio data were grouped into six periods: May to June, July to August, September, October to November, February to March, and April.

The equation used for estimating the required sample size was:

$$n = \frac{z_\alpha^2 AN}{\left(\frac{B^2 100(N-1)}{(100+A)^2} + z_\alpha^2 A \right)}$$

where A = the estimated number of calves per 100 animals, N = the total population in the mixed herds in the area to be sampled, z = the two-tailed value from the normal distribution, and B = the precision per 100 animals.

In estimating the sample size, the following values of N were assumed for each area:

a) a population of 2,000 in Area I prior to 1975.

b) a population of 1,500 in Area I after 1975.

c) a population of 6,500 in Area II prior to 1975.

d) a population of 4,000 in Area II after 1975.

The confidence intervals around the calf ratio were calculated using the formula:

$$b = \frac{z_\alpha (a + 100)}{10} \sqrt{\frac{a\,(N - n)}{n\,(N - 1)}}$$

where z.05 = 1.96 if 95% confidence intervals are desired (two-tailed value from the normal distribution), a = observed number of calves per 100 animals in mixed herds, N = the total population in the mixed herds in the area to be sampled, and n = the total number of animals counted. Thus, a 100 (1-x)% confidence interval on a:100 will be (a-b)/100, (a+b)/100. Where herds were designated as "mixed", no correction factor was used to compensate for the inclusion of young bulls.

No calf surveys were conducted between 1981 and 1983. Beginning in 1984, a new technique developed by C. Gates for use in the Mackenzie Bison Sanctuary was adopted for use in Wood Buffalo National Park. Helicopters drive bison past observers stationed at strategic positions on the ground, and the ground observers make the counts.

In addition to the "classified counts" of calves, cow:calf ratios were obtained during naturalistic studies. Observations of interactions between wolves and bison were carried out from the ground during the following periods: 21 - 27 August 1985; 18 - 21 June 1986; 29 May - 12 June 1987; 29 May - 25 June 1988; 6 - 19

March, 29 May - 19 June 1989; 27 Sept. - 7 Oct. 1989, 18 - 24 June 1990, 21 Sept. - 3 October 1990; 3 - 19 June and 27 Sept. - 6 Oct. 1991. Over the five years, 116 days were spent following and observing bison in the field.

During winter, observations were made while travelling on snowshoes and while camping near herds that were subject to heavy predation by wolves. In summer, observations were made during extensive hikes through the area (distances travelled up to 25 km/day were not uncommon), while camping overnight in tents, or while rafting/canoeing along creeks and rivers in the Delta. The actual duration of contact with herds varied from 0.5 to 10 hours at a time. This work is described in greater detail in the predation chapter.

C. *Results And Discussion*

Calf counts made during the 1950s and from 1971-1983 indicated higher calf proportions during the 1950s than during the 1970s (Figures 32 and 33). Between 1971 and 1975, calf counts in Area I were lower than those in Area II; this trend appeared to reverse during the second half of the decade.

Records of complete calf counts were available for both Areas I and II for the five years shown in Table 21. How representative these samples are of the entire population cannot be determined; however, data suggests that in two of these years (1972, 1976) the proportion of calves was significantly higher in Area II than in Area I. Because the proportion of calves in Area I and Area II was significantly different during some years, the results from each area were analyzed separately.

The calf percentages obtained from conducting multiple surveys of the same area during the same time period were significantly different from one another in three of seven cases (Table 22). In two cases (Area I — 1976 and 1981), the calf percentages during June were significantly lower than those during August, possibly because calving had not been completed in June. The number (82) counted in Area I during 1981 is small and was probably unrepresentative. Therefore, it appears that repeated aerial surveys within a short period of time do not always produce comparable results, so differences in calf percentages between years must also be interpreted with caution. The timing of surveys is obviously critical. Adequate sample sizes, random flight patterns, and random distribution of surveyed areas are also important in ensuring that the sample is representative of the average condition. Comparison of the data from vaccination programs with data from aerial surveys assumes that samples are comparable and unbiased. This may not be the case, because the sex and age composition of corralled bison may not be representative of the population as a whole. M. Meagher (pers. comm.) noted that in Yellowstone National Park, proportionately fewer bulls than cows and calves were captured during roundups.

Significant differences in calf percentages between years were identified in both Areas I and II (Tables 23 and 24). However, the calf percentages in Area I and Area II were not correlated ($r = 0.30$, $p > 0.05$). This suggests that the factors that influence the proportion of bison calves in Areas I and II are not correlated, which may mean

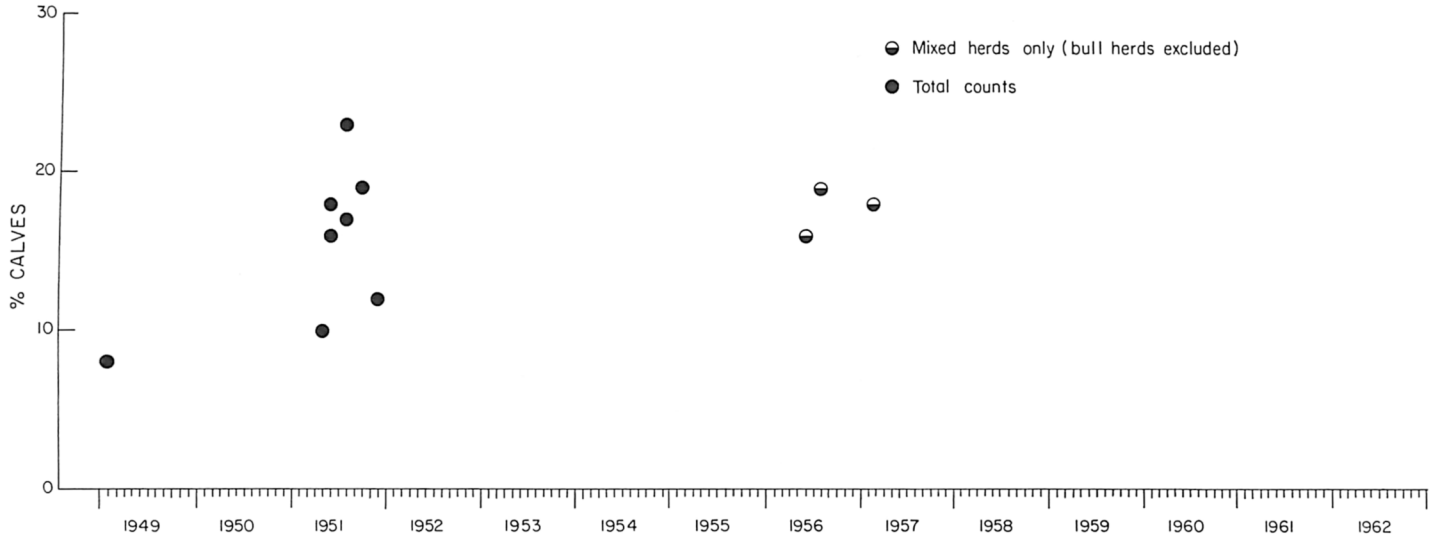


Figure 32. Calf percentages (percentage of total) determined from data collected during surveys conducted in the 1950s by Fuller and Novakowski.

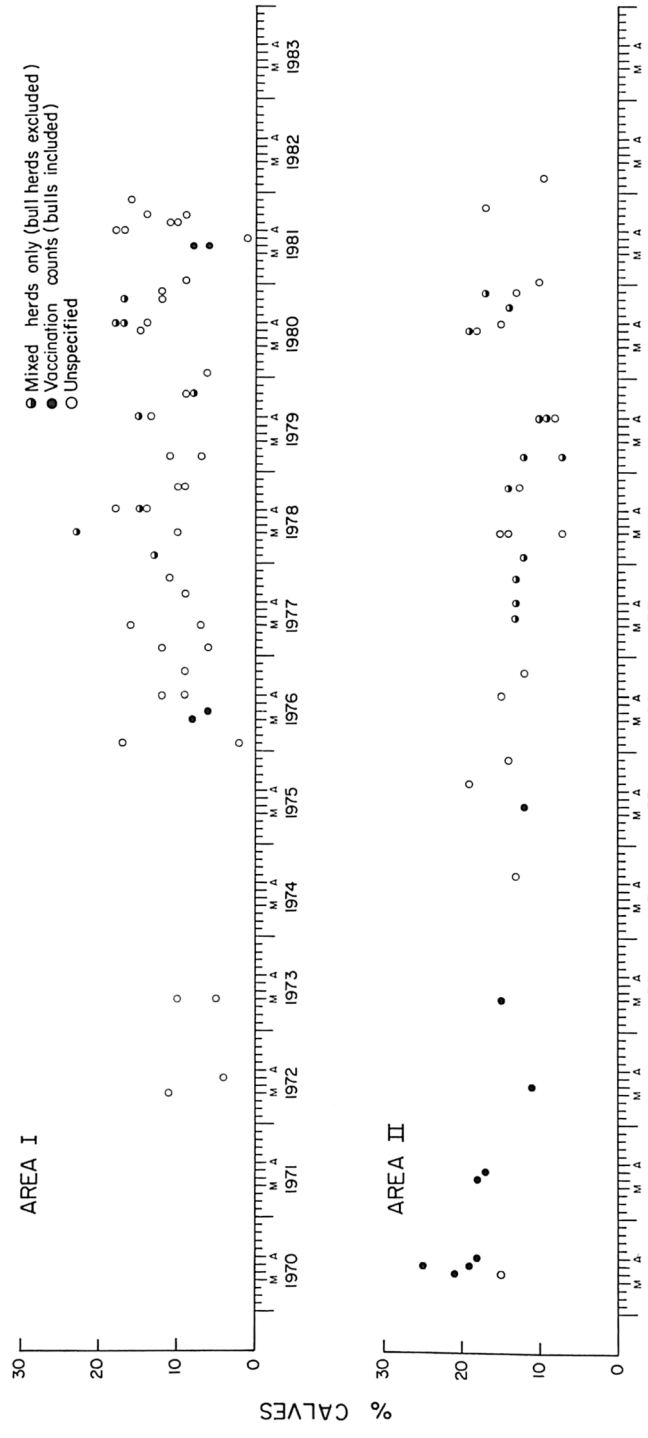


Figure 33. Calf percentages (percentage of total) determined from data collected during surveys conducted primarily in May through August, 1970-1981.

Table 21. Calf percentages (as percentage of total) in Areas I and II of Wood Buffalo National Park, 1972-1980. The largest sample was used if more than one survey was conducted during a sampling period (June to August).

	Area I			Area II				
	Adults	Calves	Calf percentage	Adults	Calves	Calf percentage	X^2	p
1972	674	27	3.9[1]	4299	518	10.8	32.75	0.00
1976	1026	100	8.9	959	162	14.5	16.92	0.00
1978	143	32	18.3	983	165	14.4	1.84	0.18
1979	222	34	13.3	969	100	9.4	3.50	0.06
1980	316	53	14.4	1970	421	17.6	2.37	0.12

[1] Survey from Raup Lake area - 24 June 1972; no explanation available for this low figure.

Table 22. Chi-square values and probability levels for comparison of the proportion of bison calves among multiple samples taken in the same area during the same year in Wood Buffalo National Park, June - August, 1970-1981.

	n	X^2	p
Area I			
1976	3	8.370	0.015
1980	2	1.270	0.261
1981	5	39.110	0.000
Area II			
1970	4	20.650	0.000
1971	2	0.550	0.459
1979	2	0.095	0.759
1980	2	2.317	0.128

Table 23. Calf percentages in bison herds in Area I, 1972-1981, and the other years that had significantly fewer calves. If more than one sample was taken during a sampling period (June to August) the largest number was used. No data are available for the missing years.

Year	Calf percentages (of total Bison)	Years with significantly fewer calves
1978	18.3	1972, 1981
1980	14.4	1972
1979	13.3	1972
1976	8.9	1972
1981	6.8	-
1972	3.9	-

Table 24. Calf percentages in bison herds in Area II, 1970-1980, and the other years that had significantly fewer calves. If more than one sample was taken during a sampling period (June to August) the largest number was used. No data are available for the missing years.

Year	Calf percentages (of total bison)	Years with significantly fewer calves
1970	20.4	1979, '72, '75, '78, '76, '73
1980	17.6	1979, '72
1971	16.6	1979, '72
1973	14.7	1979, '72
1976	14.5	-
1978	14.4	-
1975	11.7	-
1972	10.8	-
1979	9.4	-

either that the surveys are not comparable or that local factors (e.g., predation) differentially influence observed calf/cow ratios. Since the number of surveys varied, the highest counts were used to standardize results.

There appears to be a negative correlation between the severity of snow conditions from the previous winter and calf production, but the relationship is not statistically significant. A regression calculation could not be made for the data from Area I. In Area II, the slope of the regression line was negative (-0.541), but was not significantly different from zero ($F = 5.23$, $p > 0.05$; Figures 34 and 35).

The use of a contingency table may not be desirable for analysis of calf-percentage data because the assumption of independence between snow depth and calf mortality may be violated. Also, if individuals of particular sex- and age-classes tend to form herds, then the age and productivity of an individual is not independent of that of other bison in the herd. This data could also be analyzed by using the herd as the sampling unit and calculating a regression line (fitted through the origin) for the relationship between herd size and the number of calves. The slopes of the regression lines for different herds could then be compared. An initial attempt to correlate calf production with herd size showed that there were no differences between large and small herds (Tempany 1976); however, the number of large herds sampled was small. Subsequent ground observations from 1985 to 1991 did show that smaller mixed herds often contained higher percentages of calves.

Calf surveys were not consistent with respect to whether bulls were included or excluded. Therefore, estimates of young/adult ratios were influenced by the methods used during data collection. Furthermore, variable rates of actual yearling

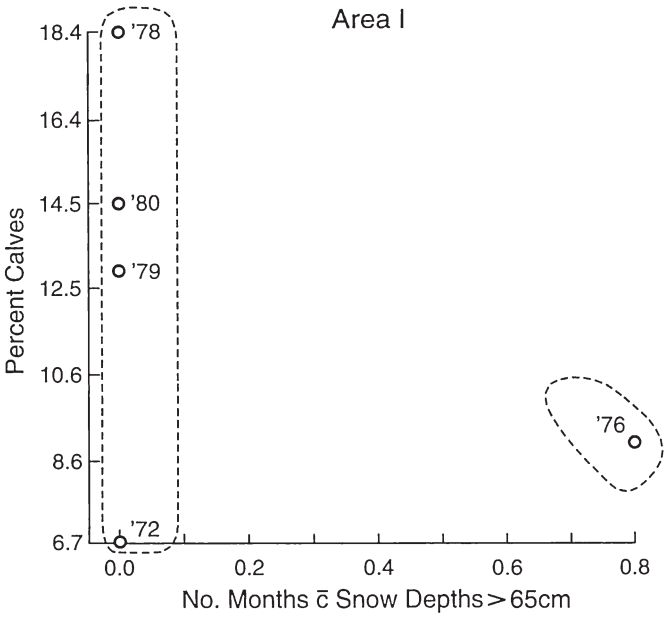


Figure 34. Relationship between the duration of the period of critical snow depth (≥65 cm) and the percentage of calves the following summer in Area I, 1970/71 to 1980/81.

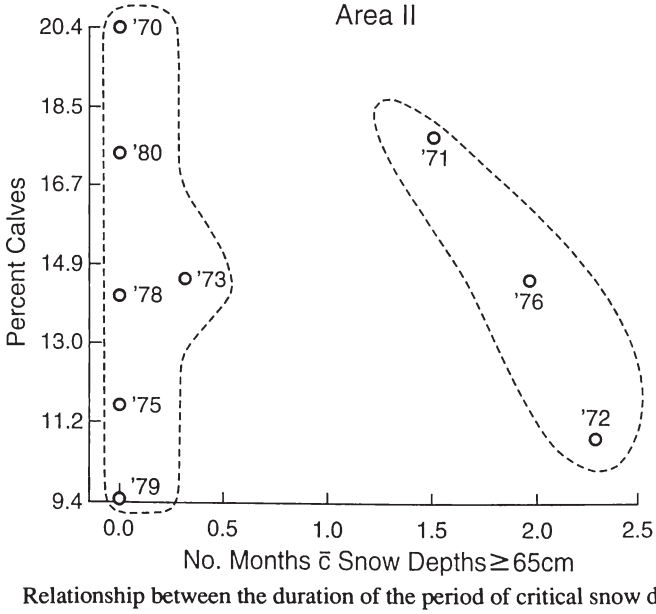


Figure 35. Relationship between the duration of the period of critical snow depth (≥65 cm) and the percentage of calves the following summer in Area II, 1970/71 to 1980/81.

survival influences results of calf productivity. Productivity during one year may be lower than during another, but if the yearling survival that year is also lower, the productivity would appear to be higher than it actually is in the comparison between years. Similarly, calf production may appear to be depressed if yearling and subadult survival is higher than usual. Thus an apparent change in productivity may result from a change in the rate of survival of the yearling class from one year to another, rather than from an actual change in fecundity. Comparisons between years can be made only when observations of other parameters are followed as well. Some interesting results have been obtained in the Slave River Lowlands area (Jalkotzy 1979, Van Camp and Calef 1987), where a calf crop of 22% during June 1978 subsequently declined to 11% during November and 6% during March. For the same herd, during the spring of a different year, these investigators recorded a calf crop of 18%, with a relatively high summer to midwinter survival rate; the calf survival rate declined to 10% during January, followed by a precipitous decrease to 6% during March. Because bison in portions of Wood Buffalo National Park (northern areas) generally exist in less discrete and identifiable herds than do those in the Slave River Lowlands, it is more difficult to quantify changes in calf survival.

Fuller (1966) showed that in bison, reproductive vigour was highest between three and twelve, or possibly 15, years of age. If there are bulls and yearlings in a population and the sex ratio is 50/50, an observed calf/non-calf ratio of 1/5 [such as the mean calf percentage of 21.5% seen in the Mackenzie Bison Sanctuary population between 1975 and 1977 (Calef 1984)] is high. On the other hand, if the calf/cow ratio is based on the number of calves/100 cows, then a ratio of 1/5 is low. Because all calculations done on aerial surveys have been made from counts of the number of calves/100 non-calf units, they do not accurately reflect fecundity. During the mid 1980s, counting methods were revised to obtain accurate calf/cow ratios by recording sightings from the ground and this was certainly a positive change.

The estimated sample sizes required for 95% confidence intervals for predetermined levels of precision are listed in Table 25. When calf percentages are in the 10-20% range in mixed herds (as in warden surveys), the minimum acceptable margin of variation should not exceed ± 2 calves/100 animals, to ensure that the sample is within ± 5% of the population. As previously shown for actual calf percentages the presence and abundance of bulls and yearlings in sampled herds can significantly affect calculations; presumably a herd's composition can also affect the accuracy of confidence limit estimates.

This method assumes that counts are random. However, most surveys in which a minimum sample size is needed are probably intuitively directed towards areas in which animals are the most readily available. Thus, a search for mixed herds in open areas that are frequented by large herds could bias the sample, if in fact, smaller herds in more limited ranges have either higher or lower calf production and/or survival than do larger herds. Because the formula produces an upper limit for the estimate of the necessary sample size, samples should consist of distinct animals and not of

Table 25. Estimated sample size, at five levels of precision, for estimating the percentage of calves in mixed herds with 95% confidence.

	Area I					Area II				
	±1/100	±2/100	±3/100	±5/100	±10/100	± 1/100	±2/100	±3/100	±5/100	±10/100
May-June										
1972	15.8	829	549	264	77	-	-	-	-	-
1973	12.2	718	446	202	57	-	-	-	-	-
1976	9.8	546	342	155	44	-	-	-	-	-
1977	24.8	819	642	380	130	12.6	1034	562	229	60
1978	17.6	725	522	276	86	-	-	-	-	-
1981	17.1	716	512	268	83	24.7	1698	1078	497	141
n required:		829	642	380	130		1698	1078	497	141
July-August										
1970	-	-	-	-	-	31.2	2416	1523	698	197
1971	-	-	-	-	-	23.8	1976	1158	498	136
1972	5.5	414	220	88	23	-	-	-	-	-
1976	13.1	635	425	206	61	20.6	1506	912	403	111
1977	-	-	-	-	-	12.6	1032	560	228	60
1978	26.1	831	660	397	139	15.0	1190	669	279	75
1979	14.8	673	464	233	70	-	-	-	-	-
1980	17.0	715	511	267	83	19.0	1417	840	365	100
1981	24.4	815	636	374	128	-	-	-	-	-
n required:		831	660	397	139		2416	1523	698	197

Table 25. Continued.

	Area I					Area II				
	±1/100	±2/100	±3/100	±5/100	±10/100	± 1/100	±2/100	±3/100	±5/100	±10/100
September										
1975	26.3	833	662	400	140	-	-	-	-	-
1981	14.8	673	465	234	70	-	-	-	-	-
n required:		833	662	400	140					
Oct.-Nov.										
1975	20.5	768	575	318	103	-	-	-	-	-
1976	8.9	516	315	141	39	12.2	1007	544	220	58
1977	12.6	624	414	199	58	-	-	-	-	-
1978	13.4	642	432	211	62	11.4	949	507	203	53
1979	4.6	333	180	73	19	-	-	-	-	-
1981	14.0	655	446	220	65	23.9	1666	1048	479	135
n required:		768	575	318	103		1666	1048	479	135
December										
1981	23.0	799	615	354	119	-	-	-	-	-
Feb.-March										
1975	20.9	773	581	324	105	-	-	-	-	-
1977	12.9	630	420	203	59	11.8	977	524	211	56
1978	9.2	528	325	146	41	8.8	756	387	151	39
1979	8.3	494	298	131	36	-	-	-	-	-
1980	12.1	611	402	191	55	14.3	1141	635	262	70
1981	12.8	629	419	203	59	12.0	992	535	216	57
n required:		773	581	324	105		1141	635	262	70

recounted animals. If recounted animals are used, the upper range of the confidence limits must be raised. For the calculations in this report, high upper limits were used to increase the precision.

From the data collected by wardens during aerial surveys of calves between 1971 and 1981, it was concluded that attempting to develop a solid information base on calf production from aerial surveys was not possible. The small sample sizes, clumped distribution of animals, variable visibility of calves in small versus large herds, lack of standardization (in the inclusion of bulls, bull herds, and lone animals), use of data derived from anthrax surveys or from corralled herds, and the variation in the timing of surveys all contributed to a margin of error that makes the results essentially meaningless. Consequently there is too much uncertainty in the data to interpret fluctuations in calf production recorded in Area I and Area II from 1971 to 1981. The usefulness of these comparisons was to set the stage for more rigorous data collection on calf production. This was done on ground counts.

The data summarized in Table 26 were collected between 1985 and 1991 using more standardized survey techniques, which had been developed for counting bison calves in the Mackenzie Bison Sanctuary (see Methods). The results from follow-up ground observations made while following herds during 1989-1991 are summarized in Table 62 (see Predation chapter).

Using conservative estimates in the correction factor, and on the basis of results obtained by using helicopters to herd bison past observers on the ground, it was concluded that between 1985 and 1991, the ratio of calves/100 cows ranged from 22/100 during 1989 to 32/100 during 1986.

Examination of the results of recent calf counts, particularly those obtained using helicopters for herding, show that the ratios of number of calves/100 cows are roughly comparable with those obtained by Fuller during counts made along park trails between 1950 and 1953 (Fuller 1966). The two may not be strictly comparable because the latter were conducted in areas with heavy vegetation. In the Delta, aerial surveys resulted in calf percentages of 12-23% during 1951, 12-24% during 1952, and 21% during 1953. During the counts made in the summer of 1951, the calf percentages were 18% and 16%. When the percentages from the 1950s are compared with those from the late 1980s, it appears that the latter are marginally lower. It should be remembered that wolves were controlled between 1950 and 1953 (average of 66 recorded as being killed each winter), whereas they were not controlled during the 1970s and 1980s. It is likely that the total number of bison, given the decrease in the bison population since the 1950s, were higher during the former period than during the latter.

The problem with this reasoning is that the methods of obtaining calf counts varied greatly. Ground and air counts cannot be compared. It is only after a systematic means of obtaining ground counts was developed in 1986 that a year to year comparison was possible. Furthermore, herd composition is the most important factor influencing calf percentages. The only meaningful parameter is to express calf ratios in terms of the number of calves per 100 cows greater than 2-years old. This method was used in the cow/calf studies carried out between 1985 to 1991 (see chapter VII).

Table 26. Results of standardized segregation counts of bison in the Peace-Athabasca Delta. Counts were conducted by the Warden Service in Wood Buffalo National Park from mid June in each year from 1985 to 1991.

Year	Total Bison	Cows Total	Cows %	Calves Total	Calves %	Yearlings Total	Yearlings %	Bulls Total	Bulls %	Calves/ 100 cows	Yearlings/ 100 cows
1985	1486	723	49%	201	14%	194	13%	387	25%	28/100	27/100
1986	2792	1426	51%	447	16%	298	11%	621	22%	32/100	21/100
1987	2241	1238	55%	369	17%	238	11%	396	18%	30/100	19/100
1988	2802	1436	51%	352	13%	126	4%	888	32%	25/100	9/100
1989	1880	1089	58%	235	13%	41	3%	515	28%	22/100	4/100
1990	1334	854	64%	258	19%	31	2%	191	14%	30/100	4/100
1991	1223	734	60%	225	18%	50	4%	214	18%	31/100	7/100

V Disease and Poaching 1971 - 1991

1. *Disease*

A. *Introduction*

An historical perspective of the bovine diseases in Wood Buffalo National Park has been presented (see Table 1). These diseases are known to have important implications in the population dynamics of ungulates. In elk, for example, cows newly infected with brucellosis will abort approximately 50% of the time in naturally infected herds and from 50-70% of the time in artificially inoculated females (Thorne et al. 1978). For elk this means roughly the loss of one out of every eight calves.

The mode of transmission of brucellosis, is through direct contact with reproductive products, such as tissue from after-birth, still born fetuses, fetal fluids and newborn calves born to cows carrying the bacteria (Thorne et al. 1978; Tessaro 1987, 1989; Tessaro et al. 1990; Peterson, M.J. 1991).

Bovine tuberculosis is similarly caused by a bacterium. It can spread within a population through ingestion of food or water contaminated by the bacterium, or through inhalation of sputum droplets expelled by coughing. It can be passed on to offspring via milk or through the placenta.

Tuberculosis is a disease that becomes progressively debilitating with age and can affect the general health of an animal, hence may well render prey more susceptible to predation. The prevalence of a third major disease, anthrax, was discussed earlier. Manipulation of bison to vaccinate against the disease was considered an important mortality factor during the management era. "Bison deaths attributed to anthrax" are summarized in Table 17. Since 1971, outbreaks occurred in 1978 (48 carcasses found in the Park, 78 found in total) and 1991 (32 carcasses found in the Park). Anthrax may well be an important mortality factor and much of it may have gone undetected in remote areas.

B. *Methods*

During field studies from 1985 to 1991, observations of crippled or otherwise debilitated animals were noted, but this does not give a true representation of the incidence of disease in the population. More importantly, Tessaro (1987) necropsied 164 bison that were found dead between June 1983 and August 1985.

Seventy-two carcasses were suitable for analysis. Tessaro's study was not based on stratified sampling techniques of various age and sex classes, but were restricted to opportunistic sampling. For details the reader should refer to Tessaro (1987). Tessaro's work was an extensive review of the prevalence of disease in the bison and his findings are summarized below.

C. *Results and Discussion*

From necropsy and tests of 72 bison carcasses, 18 (25%) had evidence of brucellosis and 15 (21%) had tuberculosis. Two carcasses had concurrent infections (Tessaro 1987). Prevalence of disease, based on the above results, at the 95% confidence limits were set at 15.5 to 36.6% for brucellosis and 12.1 to 32% for tuberculosis.

Hunters accounted for 56 of the 72 carcasses examined. Fifteen bison killed by hunters or 27% of the total had brucellosis and nine (16%) had tuberculosis. Tessaro further reported that four out of 13 wolves, one of 37 red foxes and one of five moose examined contained brucellosis-causing bacteria and none of the other (i.e., non-bison) species tested positive for tuberculosis. Field observations from 1985 to 1991 confirmed the presence of crippled bison in the population. In a sample of 3,412, 19 animals, or about 1% showed moderate to severe signs of lameness. In technical terms, Tessaro has described one case as a result of "...loss of articular cartilage with eburnation or lysis of bone, synovial villus hypertrophy and pannus formation, thickening and distention of the joint capsule, and.....presence of a translucent, viscous, yellow fluid containing small flecks of debris, and it was in the joint space and distended tendon sheaths distal to the joint" (Tessaro 1987:147). Obviously, much that goes on in the animal cannot be perceived by the field worker. If various degrees of emaciation and "slower" limb movements are included in critical field observations, the 1% figure increases to about 2%.

The severe cases that were observed appeared so debilitating that the animals undoubtedly succumbed from effects of old age and disease. Tessaro (1987) estimated that 6% adult bison mortality was due to tuberculosis. Fuller (1966) based on observations at bison slaughters, estimated a loss of 4-6%. Neither sources are considered accurate because it is difficult to follow up on disease related deaths in the wild.

Chronic infections are maintained in infected bison and the intermingling of individuals suggests that the diseases are well established within the whole population of the region. This consideration is important when the different population trends north and south of the Peace River are considered.

Calves observed at close range from 1985 to 1991 appeared, for the most part, to be healthy. In two instances it was noted that calves appeared to be somewhat less than optimal in appearance of "good health" (Carbyn, field notes). Tessaro (1987) reported one case of a calf with encephalitis. The calf, when attacked by wolves, stood in a "saw-horse" position, with head lowered and would not flee. This animal was quickly killed. We observed no similar instances in 116 days field work, so Tessaro's observations could be an unusual case. It is not known whether

calves are severely weakened *in utero* by disease and if they are affected, succumb either at parturition, or become vulnerable to predation shortly after birth.

2. *Poaching*

A. Introduction

Killing of bison by human hunters in Wood Buffalo National Park is illegal. Because of the size of the Park, not all infractions are detected by law enforcement officers. The degree to which laws are broken varies, depending in part on such factors as environmental conditions (i.e., snow depths, freeze-ups), social conditions (i.e., availability of jobs, unemployment, relationship of Park authorities with native people, number of trappers out on the trapline, etc.), and availability of manpower to enforce the regulations.

B. *Methods*

It is not possible to quantify the year-to-year variations in the losses of bison to poaching activities. Estimates are based on known convictions and cases where poaching was suspected. Data contained in such reports did not specify whether there were follow-ups or investigations and the laying of charges.

C. *Results And Discussion*

At the time of the establishment of Wood Buffalo National Park in 1922, 119 native residents were allowed to pursue their traditional hunting and trapping rights in the Park area. Traditional land use rights were guaranteed to those individuals, their widows and direct descendants. The rights continue to this day, however, the numbers of individuals has changed. The current limit has been set at 325.

Throughout the years some bison apparently have been illegally killed in the Park (Tessaro 1987; Park files). There has been a consensus of opinion among many of the Park wardens that such activity, in the past, may be less generally engaged in by those who had legal trapping rights in the Park. It appears that much goodwill was established between Park authorities and native residents of the area since the mid 1980s when, as a result of Land Claim Settlements with the Fort Chipewyan band, a Wildlife Advisory Board was established. This board created a legal basis for orderly input and discussion of all wildlife-related management issues that pertain to native people in the southern portion of the Park.

VI Wolves

The period of steep decline of the bison population (beginning around 1970), was preceded by several decades (1935 to about 1968) of predator control programs. Opinions about the impact of wolves on bison numbers at the time varied. J.D. Soper in the 1940s believed that wolves had a major impact (Soper 1945), while W.A. Fuller (1960) thought that in the late 1940s and 1950s predation did not seem to have a major impact on the Park's bison population; a view that he still held in 1991 (Fuller, W.A. 1991). Fuller (pers. comm.) seldom saw a wolf from the air (maybe one every 10 flying hours). Considering the eminence and excellent reputation of this biologist, we concluded that wolf numbers in the 1980s and 1990s changed considerably from those of the 1950s. A parallel can be seen in the Mackenzie Bison Sanctuary. Wolf numbers during initial years of bison number increases were either lower, or predation was less pronounced.

1. *Population Dynamics*

A. *Introduction*

A wolf pack has a conspicuous presence in an area (tracks, kills, howling) and the colour phases allows recognition of population sub-units or packs. Numbers in Wood Buffalo National Park were determined from various sources. Warden aerial surveys of bison were intensive searches in open areas and wolves often were in close association with these herds. Counting the number of wolves seen per hour flown was one important method of obtaining an index of wolf abundance used for this study. Another important measure of wolf densities was average pack size. The larger the average pack size, the higher the densities (Rausch 1967).

B. *Methods*

Home range size for radio-collared wolves was used for the calculation of wolf densities. The polygon-perimeter method of Mohr (1947) is a useful way to compare size and shape of home range with results of other published wolf studies. Adequate measurement of home range sizes can be evaluated by plotting the cumulative number of locations in relation to the area occupied by means of a

modified "species-area" curve (Odum and Kuenzler 1955, Tester and Siniff 1965). Home range sizes are adequately defined when the curve of the area reaches an asymptote. Multiple asymptotes represented expansion, seasonal, or year-to-year shifts of home ranges (Carbyn 1980).

A second method assumes that the entire area within the polygon is probably not used by the wolves, and therefore does not give a realistic estimate of home range size. In this case, the perimeter location points are connected only if they are less than one-fourth the distance between the most distant locations (Harvey and Barbour 1965). All points farther apart are then eliminated from the home range calculations.

Further, home range size can be calculated from the geometric mean center of activity (Hayne 1949), using the mean activity radius (Dice and Clark 1953, Tester and Siniff 1965). The latter expression describes the core area of a home range. Finally, home range size can be calculated from the atypical habitat elimination method (Ables 1969). Areas distinguishable by physical features from the usual range of radio-collared wolves, and which were seldom visited by wolves, were excluded from calculations.

Frequency-distribution graphs of distances from the geometric center of activity can be used to assess territoriality, dispersal, and home range boundaries. Area use within the home range was determined by dividing the area into arbitrary units of 6.25 km^2, similar to procedures described by Tester and Siniff (1965) and Ables (1969), and plotting the frequency distribution of the number of locations in each of these squares.

Wolves were captured for radio-tracking by darting them from a helicopter using a Cap-Chur gun and immobilizing darts propelled by a .22 charge. Alouette II, J-42 and Bell 206B helicopters were used. It was possible to remove the door from the J-42, which made tracking and darting the wolves much easier than from the Alouette II. The Bell 206B likewise had better visibility for the shooter as the entire window on the shooter's side could be removed. The combination of a talented pilot, good visibility and experienced personnel, resulted in a much lower time expenditure for wolves captured in 1979-1980 than for 1978-1979.

Darts were loaded with 100 mg of phencyclidine hydrochloride (Sernylan: Parke-Davis Co.) and 50-100 mg of promazine hydrochloride (Sparine: Wyeth Laboratories) or 100 mg of xylazine (Rompun; Chemagro Inc.). Wolf packs were first located with fixed-wing aircraft before being pursued by helicopter. Once wolves were collared, data on their movements and predation rates were obtained by locating their radio signals using a fixed-winged aircraft. Collared wolves were monitored in February and March of 1978 at 2-4 day intervals and less intensively during summer from May to September 1978. Intensive tracking continued at 1-3 day intervals from January to early April 1979, in December 1979, mid January to early April 1980, December 1980 and from mid January to mid April 1981.

C. *Results And Discussion*

i) Population trends

Wolf numbers in Wood Buffalo National Park increased rapidly during the early 1970s (Table 27). From 1971 (approximately 5 years after the last official predator control activities) to 1974 (year of the major flood), wolf numbers were high. Average pack sizes observed varied from nine to 15 per pack, and the number of wolves sighted per hour of flying time ranged widely from averages of about 0.5 to four wolves per hour. From 1974 to 1986, wolf numbers were lower (average pack size 4-10; numbers sighted varied from .5 to 1.9 per hour), until 1987 when numbers began to increase again (average pack size 10-13 per year and numbers sighted per hour ranged from 1.1 to 2.6). Indices of wolf abundance dropped noticeably after 1977 (Table 27), yet there is no indication why this happened. Increases were recorded again from 1983 onward to 1990. It should be noted that although official predator control ended sometime in the mid 1960s, human killing of wolves continued. The record of kills (fur harvests) from 1971 to 1979 are 26, 4, 34, 26, 5, 38, 26, 23, and 20 respectively for an average of 22 wolves per year. In the 1980s, kills of about 20 wolves per winter were considered average. In recent years, trappers only occasionally kill wolves and the overall impact on wolf numbers is considered inconsequential.

During observations of bison herds in summer 1990, the size of wolf "hunting units" was recorded (Table 28). In spring and summer hunting units generally comprised two-four wolves, sometimes more. Ground observations at rendezvous sites revealed that pack sizes can be large. For example, in October 1990 numbers varied from 12-26 wolves per pack. We were able to determine the number of packs and total number of wolves on primary bison ranges from aerial radio-tracking and ground observations. The wolf population in the Park during the period 1971 to 1991 was estimated from 80-220. A long-term average of approximately 140 wolves in roughly 9,000 km^2 can be expected (one wolf per 60 km^2) for primary bison ranges north and south of the Peace River. This figure was obtained from looking at spacing of the number of packs in the area and from data collected on average pack size (Figure 36).

ii) Capture data and fate of collars

Forty-three wolves were captured and radio-collared from February 1978 to March 1981. Three of these were caught in snares or leg-hold traps set by local trappers; the remainder were captured with tranquillizer darts fired from helicopters (Table 29). The sample consisted of 21 females and 22 males, 27 of which were adults, and 16 of which were immature wolves younger than 21 months (Table 30). Colour phases were 15 black, 12 grey, 11 blonde, and five brown wolves. Subsequent observations of wolves from 1985 to 1991 indicated that by far the greater number of wolves sighted in the Delta were light-coloured animals.

Wolves were captured in late winter, when pups were large and often appeared to be full-grown. Wolves not readily distinguished as pups or yearlings were pooled

Table 27. Trend in wolf numbers in Wood Buffalo National Park, 1971 to 1991. Data 1975 to 1976 from Stelfox 1977 and 1977-1991 from Park records.

Year	Stage	Wolves		Total hours flown
		$\bar{X}$ Pack Size	Sightings/Hour	
1971	I	9 (119 wolves)	-	35 (Area II)
1972	I	10 (259 wolves)	-	-
1973	I	10 (447 wolves)	3.2	140
1974	I	15 (361 wolves)	3.7	99
1975	II	8 (165 wolves)	1.8	94
1976	III	6 (54 wolves)	1.9	63
1977	III	8 (103 wolves)	2.3	78
1978	III	8 (31 wolves)	0.5	64
1979	III	6 (36 wolves)	0.7	55
1980	III	10 (38 wolves)	0.8	47
1981	III	5 (18 wolves)	0.6	28
1982	IV	-	-	-
1983	IV	4 (35 wolves)	1.2	31
1984	IV	6 (15 wolves)	0.7	21
1985	IV	5 (15 wolves)	0.6	27
1986	IV	-	-	-
1987	IV	10 (41 wolves)	1.2 (16 kills)[2]	35
1988	IV	11 (33 wolves)	1.1 (13 kills)	29
1989	IV	10 (95 wolves)	2.6 (8 kills)	37
1990	IV	13 (52 wolves)	1.6 (60 kills)	33
1991	IV	9 (19 wolves)	0.6 (8 kills)	30

SUMMARY:

Stages (see Figure 9 for details)	**$\bar{X}$ pack size**	**Sighting Index[1]**
1971-1974	I - 11	3.5
1975	II - NA	NA
1976-1981	III - 7	1.2
1982-1991	IV - 8	1.3

[1] Number of wolves seen per hour flown on aerial surveys.

[2] Kills recorded during aerial surveys.

Wolves spend most of their time in close association with the bison herds and depend on bison for their major source of food.

Wolves in Wood Buffalo National Park have developed a strong search image for calves.

A cow in defence of her dead calf remains at the kill site for 2 hours before she left. Cows will continue to run aimlessly through the area for 2 days or more.

At times wolf attacks will result in injury only. Blood poisoning caused by a bacteria that is transferred into the wounds by the carnivore, will often result in death.

Wolves do kill adult bulls in winter, but throughout the study all known wolf kills in summer were calves.

Scavengers and wolf kills occurs after the packs have left. Foxes, lone wolves and ravens are the most common scavengers.

One of three calves killed by a pack of wolves near a den site along Lousy Creek. This calf was abandoned but later consumed.

Remains of a bull, having died as a result of old age, disease or both. Unlike wolf kills, such carcasses are not disarticulated.

A pack of wolves resting at a kill at a bison crossing near Lousy Creek. Size of wolves in the Park are some of the largest in North America. Males weighed an average of 50 kg while females averaged 40 kg.

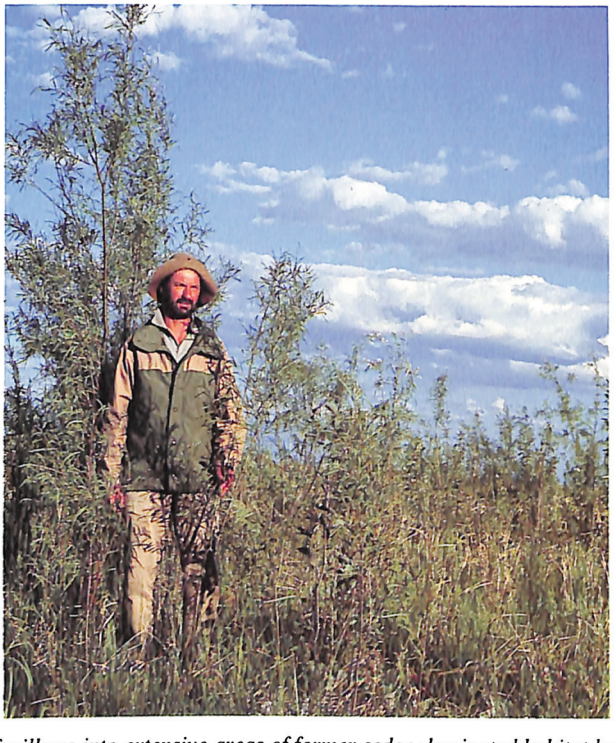
Remains of 5 bison calves killed during 2 multiple kill attacks (3,2) at a bison trail near a river crossing in early October.

Cow/calf ratios in spring (early June) averaged about 30 calves per 100 cows. This figure includes mortality from early May through to census period.

Approximately 50% of the calves survived from May to September within the major areas of bison concentrations. Similar data is not available for Area I, North of the Peace River. Early to midwinter wolf predation continued to affect calf survival, however, more adults were included in the kill rate.

Rapid loss of productive ranges has the effect of concentrating prey over fewer areas, thus likely rendering them more susceptible to predation. Loss of bison ranges is only one part of the ecosystem collapse within the region. Little is known of the effects on all the other components of the system.

Aerial view of Lousy Creek. Branch in the lower left hand corner is the only connection with Lake Claire. Evidence of drying up of the area, and hence closing off of this channel with the major body of water is shown by the debris that is accumulating at the mouth.



Invasion of willows into extensive areas of former sedge dominated habitat has occurred since the construction of the Bennett Dam in 1968. As much as 47% of some productive areas have been lost, and one study predicts that by the year 2035, two-thirds of all productive wetlands in the Delta will be lost.

Table 28. Size of wolf groups observed in the Delta of Wood Buffalo National Park during field studies in 1990.

	SPRING						FALL					
	AM			PM			AM			PM		
	4-6	6-8	8-12	12-15:00	15-17:00	17-23:00	4-6	6-8	8-12	12-15:00	15-17:00	17-23:00
Single	1	3				2				1		
Pairs		4				1		1		1		1
3 wolves				1								
4 wolves			1						1			
5 wolves												
6 wolves		1						1				
7 wolves	1		1						1			
>7 wolves (range of 8-26 in a pack)							4	1	1	2		3

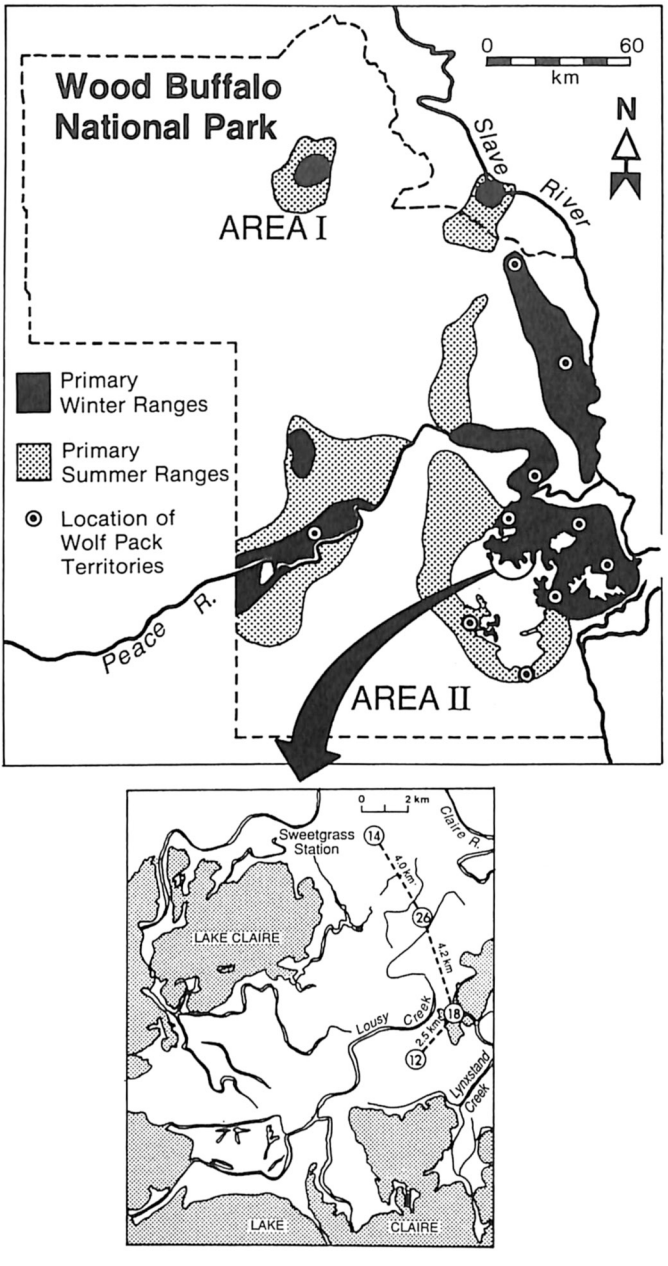


Figure 36. Generalized locations of wolf pack distribution on primary bison ranges in Wood Buffalo National Park. The lower map outlines a small portion of the Delta in which a number of wolf packs (40-70 individual wolves) occupied an area of 175 km^2 preying on bison that were highly concentrated during migration in early October 1990.

Table 29. Capture effort by helicopter for wolves collared in Wood Buffalo National Park, February 1977 to February 1981.

Month	Hours[1]	No. Of Wolves	Hours/wolf
1978			
February	16.6	11	1.5
March	15.9	9	1.8
December	5.2	0	-
1979			
January	20.5	5	4.1[1]
March	19.8	10	2.0
December	2.3	2	1.2
1980			
February	1.8	3	0.6
TOTAL	82.1	40	2.1

[1] Includes ferry time from Fort Smith to study area.

Table 30. Sex and age distribution of 43 wolves captured in Wood Buffalo National Park, 1977 to 1981.

YEAR	NUMBER OF WOLVES EXAMINED	ADULTS		IMMATURE	
		Males	Females	Males	Females
1977-78	21	7	6	3	5
1978-79	16	8	4	2	2
1979-80	5	2	-	-	3
1980-81	1	-	-	-	1
TOTALS	43	17	10	5	11

as immature wolves. Although adult males outnumbered adult females almost two to one in our study, the reverse was true for immature wolves (Table 30).

Wolf weights vary considerably over large geographic areas (Mech 1970). Average weights of adult wolves in Wood Buffalo National Park were higher than those preying on elk in Riding Mountain National Park. The average weight for adult males in Wood Buffalo National Park was 49.5 kg (n = 15, 40-59 kg) and for females was 39.5 kg (n = 7, 36-43 kg), making these some of the heaviest wolves in North America.

In 1978, 21 radio-collars were used, but some problems were experienced that year with transmitter failure. Duration of signals obtained from collars that year averaged 89 days. Two of the collared wolves were never relocated, and one wolf was monitored for 228 days. Radio-collars placed on wolves during the second winter (1978-1979) were monitored an average of 145 days, (range 10 to 257 days). Collars placed on wolves in the third year (1979-1980) continued to function throughout the subsequent winter, 1980-1981, for a maximum of 527 days.

The average "field life" of transmitters known or suspected to have failed was 184 days in 1978 (six collars) and 155 days in 1979 (13 collars). There was no transmitter failure in collars applied in 1979-1980. Collars placed on the Salt River pack (three) were all recovered and functional; one wolf carried its collar for 346 days from 18 February 1980 to 31 January 1981 when it was trapped. Two wolves in the Hornaday River pack carried double-transmitter collars from 1 December 1979 until April 1981 and possibly beyond that date as monitoring was discontinued.

Dispersal of wolves, especially in 1978 when monitoring capability was limited due to interference from other frequencies, may have accounted for some suspected transmitter failure. In at least two instances in 1978, collared wolves moved long distances (50 km or more) between subsequent radiolocations before their signals were lost, so dispersal was a distinct possibility. One wolf was eventually located near Hook Lake, Northwest Territories, 120 km north of where it had last been seen. Van Camp and Gluckie (1979) reported the long-distance movement (670 km) of a wolf captured in the Hook Lake area and killed several months later near Cold Lake, Alberta. Careful monitoring procedures in 1979, however, when signal interference was eliminated and effective monitoring range increased dramatically, suggested that transmitter failure was an important cause of signal loss.

Four of five collars examined from wolves which had carried them for at least 6 months, had been damaged. Such damage was determined by evidence of tearing of the collar band and/or tooth marks on the acrylic transmitter assembly. Three of the four collars were nonfunctional (Table 31). Two other collared wolves were observed to be missing transmitter assemblies as indicated by a dangling collar band. It is conceivable that damage inflicted by wolves on radio-collars came from other members of the pack, perhaps during times of intense social interaction such as at dens and at rendezvous sites; many of the signals disappeared during mid to late summer.

Table 31. Condition of radio-collars recovered, or observed on wolves captured in Wood Buffalo National Park from 1978 to 1980.

Circumstance	Wolf Collar #	Not Damaged	Damaged	Functional	Non Functional
On wolf more than 6 months					
Recapture	U271	*			*
Trapped	279	*			*
Trapped	285-6	*			*
Died (?)	277	*		*	
Trapped	323[1]		*	*	
Live Observ.	269	*			*
Live Observ.	271	*			*
On wolf less than 6 months					
Discarded collar	U273	*		*	
Trapped	U275		*	*	
Discarded collar	275		*	*	
Killed	322[1]		*	*	
Killed	324		*	*	

[1] Radio-collars constructed by Canadian Wildlife Service during 1979-80 were reinforced with fibreglass; none of those were damaged and all were functional.

iii) Pack size dynamics

Pack sizes in Wood Buffalo National Park are some of the largest reported in North America. According to Rausch (1967) size of packs is a measure of density, and this applies to Wood Buffalo National Park. In years of high wolf densities (1971-1974 and 1986-1991) packs were larger (Table 27) than in years of lower wolf densities (1975-1985).

Size of radio-collared packs in the Hornaday River area (Area I) was smaller than size of packs observed in the Delta (Area II), particularly those observed in the early to mid 1970s and mid 1980s to early 1990s. The largest single reported aggregation of wolves was 42 animals spotted on 20 February 1974 (Fau and Tempany 1976). There was no indication that these animals were not a single functional pack, but it cannot be ruled out that the number seen together were aggregations of several packs. Another possibility is that there were young from several females. Captive wolves are known to raise young cooperatively in captivity (Paquet et al. 1982). Other examples of large packs recorded were as follows:

- 20 wolves (January 1972)
- 22 and 28 wolves (January 1973)
- 17, 18, 18 wolves seen on one flight (April 1973)
- 26 wolves (October 1989)
- 17, 28 wolves seen on one flight (February 1989)
- 18, 12, 26 and 14 wolves seen on the ground and from the air in a 175 km^2 area (October 1990)

Large packs probably increase hunting efficiency. However, the size of potential prey may not necessarily determine pack size, as single wolves have been known to kill muskox (Gray 1970). Trappers in the Park have reported single wolves tracking and killing lone bulls (D. Dragon, pers. comm.). The killing of a large ungulate by a single wolf may not be a general occurrence and possibly occurs under an unusual set of circumstances such as deep snow, or when the prey may be physically disabled or diseased.

Pack size should increase with the size of prey until an optimum number is attained (Macdonald 1983). Optimum pack size is defined as the number of animals in a social unit, where killing is possible with the least amount of energy expenditure, and the maximum return of energy to members of the pack. Even though some wolf packs in the Park may be large, the average in winter appears to be from 12 to 16. Large packs often include immature animals, individuals that need to gain experience to become better hunters, but are a drain on the food resources acquired.

Predation is a process of energy transfer from one trophic level to another. By recording pack sizes and calculating weights of wolves, the impact packs have on the prey base can be evaluated. Biomass of a large wolf pack in the Park in the fall period is about 900 kg. This calculation is based on a pack of 24 wolves containing 12 adults/subadults, and two litters of six pups each. Equal sex ratio is assumed for both young and adults.

Radio-tracking information provided data on the splitting and recombination of packs in summer and winter (Figure 37), and on overwintering mortality. Unlike many other areas, pack sizes generally appeared to remain high from fall through to spring (Table 32). In our study, 38 collared wolves were in eight packs of three or more animals, and five wolves captured as lone wolves or pairs were radio-tracked for periods of several days to 75 weeks. Fewer groups were monitored after 1979 due to more intensive tracking of the Hornaday River pack for purposes of behaviourial studies and determining predation rates. The mean number of wolves in two radio-collared packs (the Hornaday River and Lake Claire packs) was 11 from winter 1977-1978 to 1980-1981.

Information on pack size and dynamics for the Hornaday River pack in winters 1978-1979, 1979-1980, and 1980-1981 was derived mainly from observations of collared wolves and their associates. Pack size during that time varied from 8-14 wolves in early to midwinter, and from 6-10 in late winter. These figures are lower than for wolves in the Delta area, south of the Peace River in 1985 to 1991, a time when wolf densities were higher. Pack sizes ranged from 12-26.

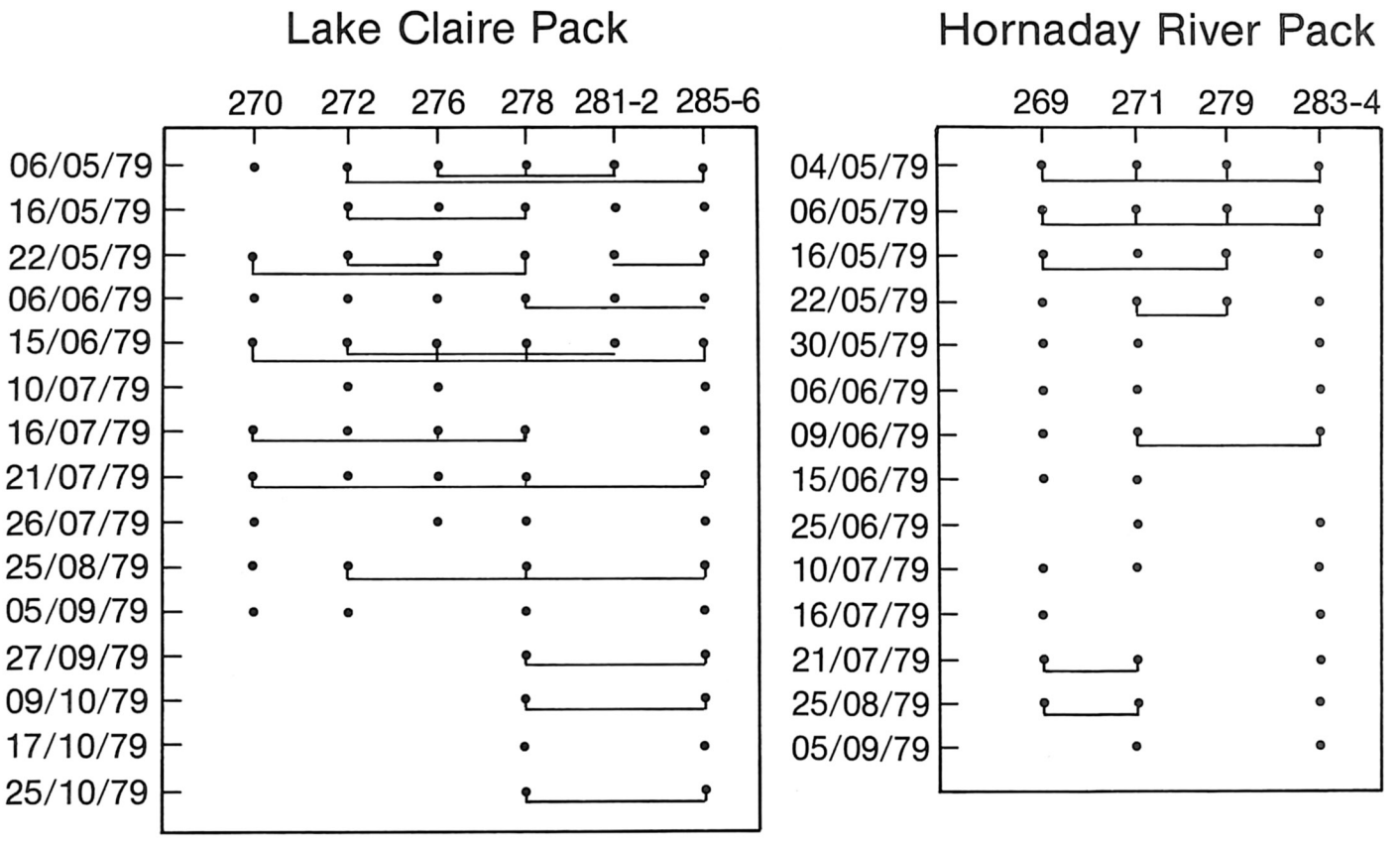


Figure 37. Association between pack members of the Lake Claire and Hornaday River pack members in the summer, 1979.

Table 32. Maximum number of wolves observed in packs in early, mid, and late winters 1977-1978 to 1980-1981, on primary bison ranges of Wood Buffalo National Park. This was a period when overall wolf densities in the Park were low.

YEAR	LOCATION	PACK DESIGNATION	MAXIMUM PACK SIZE OBSERVED		
			Early winter (Nov.-Dec.)	Midwinter (Jan.-Feb.)	Late winter (Mar.-Apr.)
1977-78	Lake Claire	Lake Claire	14	13	11
	Welstead Lake	Welstead Lake			8
	Baril Lake	Baril Lake		9	
	Hay Camp/Darough Creek Prairies	Hornaday River		8	8
	Darough Creek Prairies	?		5	
	Murdock Creek Meadows	Murdock Creek			10
	Point Providence	Point Providence	9		
	Salt Plains	Salt River	13		3
1978-79	Lake Claire	Lake Claire		12	16
	Revillon Coupe	?		7	
	Baril Lake	Baril Lake	8	7	6
	Hay Camp/Darough Creek Prairies	Hornaday River	14	14	10
	Murdock Creek Meadows	Murdock Creek	11		8
	Salt River	Salt River		5	

Table 32. Continued.

YEAR	LOCATION	PACK DESIGNATION	MAXIMUM PACK SIZE OBSERVED		
			Early winter (Nov.-Dec.)	Midwinter (Jan.-Feb.)	Late winter (Mar.-Apr.)
1979-80	Baril Lake	Baril Lake		6	
	Mamawi Lake	Mamawi Lake		9	
	Hay Camp/Darough Creek Prairies	Hornaday River	12	14	12
	Murdock Creek Meadows	?		4	
	Point Providence	Point Providence	7	7	
	Salt Plains	Salt River	6	7	
1980-81	Lake Claire	Lake Claire		9	
	Baril Lake	Baril Lake		9	
	Hilda Lake	?			9
	Birch River	?		8	
	Hay Camp/Darough Creek Prairies	Hornaday River	7	9	8
	Murdock Creek Meadows	?		6	
	Salt Plains	Salt River	7		

In 1978-1979, pack size of the Hornaday River pack decreased from 14 in early December to 10 by mid February (Table 32). Although mortality may have accounted for this decrease, observations of collared wolves indicated that splitting of the pack occurred. From 3-15 March and 6-11 April, the Hornaday River pack split into at least two groups. Male no. 271 travelled alone from 3-15 March; the remaining collared segment of the pack (females no. 269, no. 279) of six wolves, split off from the main pack of 10. The pack also separated briefly late in March and again from 6-11 April when male no. 283-4 split off with four others. Track and scat evidence indicated that three-four wolves (whose affiliation was unknown) travelled within the winter range of the Hornaday River pack.

Observed pack size for the Hornaday River pack increased from 10 early December 1979 to 14 in late January 1980, then decreased to 10 by early April 1980. In late December 1979, the pack split into at least two groups, as the two collared wolves (females no. 346-7, no. 348-9) travelled together, but separate from the rest of the pack. During late January 1980, the main pack (10-12 wolves) travelled south into the Peace-Athabasca Delta, but at least two wolves, including female no. 346-7 remained in the Hay Camp-Darough Creek prairies. From mid February on, pack size varied from 8-12 wolves. Unlike 1978-1979, when the pack was more cohesive, and a larger number of collared wolves made identification of pack members possible, it was difficult to determine which wolves left and joined the pack during 1979-1980.

Observations of the Hornaday River pack during winter 1980-1981 suggested that a major splitting or reduction of the pack had occurred since the previous winter. Pack size remained constant from six-seven wolves throughout December, although on 31 December female no. 348-9 had split off and joined an unidentified group of two others. This wolf rejoined the main group sometime before 21 January. From late January to early April pack size varied from six-nine wolves. Collared wolves did not separate from the pack until 26 March, when female no. 346-7 left the pack of six wolves and did not rejoin until 4 April.

In each winter from 1978-1979 to 1980-1981, there was evidence of the presence of "non-pack" wolves apparently loosely associated with the territory of the Hornaday River pack. On 21 and 22 March 1979, a black wolf travelled on the trail 2-3 km behind the main pack moving between kills. During late March 1980, two black wolves were observed with male no. 323[3]. The three wolves were within the composite winter range of the Hornaday River pack. From 15-18 February 1981 a black wolf was seen in close proximity, but not with the Hornaday River pack (seven wolves). The wolf fed on a bison carcass killed by the pack, but only after the pack had moved away from it. On 15 February this wolf ran away from the

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3 This wolf was one of the surviving Salt River pack, which was attacked by the Hornaday River pack in February 1980 (see subsequent discussion).

approaching pack and appeared "extremely nervous." On 22 February, the pack was within 1 km of what seemed to be two non-affiliated wolves. Upon detecting the pack, these two wolves ran in different directions away from the pack, which had not noticed the two. At the same time, a single black wolf was observed 3 km north of the two groups.

iv) Space utilization

Observations of wolves seen during the spring and fall period of 1990 are summarized in Table 28. The average pack size (including singles) in the spring was three animals per observation, while in the fall the average pack size was 12 animals per sighting. Many of the fall observations were made at rendezvous sites where sizes of four different packs in a 5-day period were 12, 14, 18 and 26. These packs occupied an area of about 175 km^2, or one wolf per 2.56 km^2. Two packs were seen from the air, and two were seen from the ground. Straight line distance from the location of the first pack to the last was 8 km. Distances between the packs were about 2.5, 4.0 and 4.2 kilometres (see Figure 36). None of the packs was radio-collared, so the possibility existed that the pack of 26 actually was the 12 and 18 (minus 6) seen on the previous day. Colour phases and the packs' locations made this unlikely, but the possibility cannot be ruled out. The numbers were therefore a minimum of 40 wolves, but more likely 70. In the fall of 1991, three packs were heard howling at three different rendezvous sites each about 2 km apart. This again indicated a concentration of wolves in one area of the Delta was less than one wolf per 3 km^2.

In fall 1990, it was obvious that at least two packs (the northernmost with pack sizes of 14 and 26) were aggressive toward each other when individuals of one pack approached another. However, the southernmost packs with 26, 18 and 12 individuals in each social unit, were apparently not as aggressive. Similarly, in October 1991, on three different occasions, single, two and three wolves travelling together from one pack were seen to travel in the close proximity to neighbouring packs without any indication of interpack aggression. These ground observations were made in the Delta (Area II) while aggression was observed in radio-collared wolves north of the Peace River (Area I) in winter.

Annual home range sizes for 22 collared wolves were determined from locations gathered throughout the year, varied from 220 to 2,730 km^2, and averaged 795 km^2 (Table 33). Unlike home range calculations for wolves in Riding Mountain National Park (Carbyn 1980), asymptotes were not readily apparent at any time of the year and likely reflected seasonal changes in home range size (see below). Ballard et al. (1981) noted a similar continual increase in home range size for wolves, and concluded that although a pack occupied the same general area from year to year, their use of outlying areas changed by season and year.

Winter home range sizes were similarly determined for eight packs on primary bison ranges of the Park from 1977-1978 to 1980-1981 (Table 34). Mean home range size during this time was 728 km^2. Home range size for packs could not be

Table 33. Annual home range size of 22 collared wolves on primary bison ranges of Wood Buffalo National Park, as determined by polygon perimeter method.

Locality	Wolf Number	Year	Number of Locations	Home Range Size (KM^2)
Peace-Athabasca	U268	1977-78	8	707.4
Delta	U270	1977-78	16	1026.0
	U271	1977-78	20	379.1
	270	1978-79	14	395.5
	272	1978-79	16	219.2
	276	1978-79	15	240.3
	278	1978-79	19	476.5
	281-2	1978-79	19	350.2
	285-6	1978-79	22	406.5
Hay Camp -	U215	1977-78	15	714.6
Darough Creek	U262	1977-78	11	190.8
Prairies	269	1978-79	61	1101.7
	271	1978-79	43	942.2
	279	1978-79	49	793.7
	283-4	1978-79	25	1234.7
	346-7	1979-80	105	2142.8
	348-9	1979-80	105	2731.1
	346-7	1980-81	79	754.6
	348-9	1980-81	85	841.7
Salt Plains	U259	1977-78	17	439.6
	323	1979-80	52	544.9
	323	1980-81	23	895.7

Table 34. Winter home range size of eight collared wolf packs on primary bison ranges of Wood Buffalo National Park, 1977-1978 to 1980-1981, as determined by polygon perimeter method.

Pack	Collared Wolves	Year	Number of Locations	Winter Home Range Size (Km^2)
Lake Claire	U270, U271, U273	1977-78	21	1040
Welstead Lake	U268	1977-78	8	265
Hornaday River	U215	1977-78	7	135
Salt Plains	U259	1977-78	6	90
Lake Claire	270, 272, 276, 278, 280, 281-2, 285-6	1978-79	14	300
Hornaday River	269, 271, 279, 283-4	1978-79	50	802
Hornaday River	346-7, 348-9	1979-80	101	2393
Hornaday River	346-7, 348-9	1980-81	84	860

determined in summer because wolves during this time were often separated and difficult to monitor.

Calculations of home range size for wolves in the Hornaday River pack from 1978-1979 to 1980-1981 using the various methods showed considerable variation (Table 35). The polygon-perimeter method in all cases yielded the largest estimate, followed by the atypical habitat elimination methods (because it was based on the former), the modified minimum-area method, and the mean activity-radius method. Within the limitations of circular home range boundaries (Sanderson 1966) the latter method was particularly sensitive to the frequency with which wolves occupied portions of their home range, although it, like the other methods, was considered only an approximation of the actual home range.

Sample size was often inadequate to compare winter and summer home range size using the conventional polygon-perimeter method. As an alternative, the mean activity radius, or mean distance between all location points and the geometric activity center (geometrical mean of all location points) was used to compare winter and summer home range sizes of individual wolves (Tables 36 and 37).

This information showed that home ranges of wolves were larger in winter than in summer in the Peace-Athabasca Delta (Lake Claire pack), and were generally smaller in winter than in summer in the Hay Camp-Darough Creek prairie (Hornaday River pack). The importance of this will be discussed in the foraging strategy differences between areas north and south of the Peace River in a later

Table 35. Home range size of collared wolves in the Hornaday River pack, Wood Buffalo National Park, 1978-1981.

		Winter home range size (km^2)				Summer home range size (km^2)[5]		
WOLF NUMBER	**YEAR**	**Polygon Perimeter**[1]	**Modified Minimum Area**[2]	**Mean Activity Radius**[3]	**Atypical Habitat Elimination**[4]	**Polygon Perimeter**	**Modified Minimum Area**	**Mean Activity Radius**
269	1978-79	807.8	481.4	298.4	665.2	562.6		572.3
271	1978-79	703.1	336.6	221.6	627.0	597.1		506.6
279	1978-79	724.2	336.6	254.3	627.0	89.6		346.2
283-4	1978-79	92.5		171.9	92.5	1174.0	193.1	669.3
Pack total	1978-79	802.0	558.9	307.8	726.0			
346-7	1979-80	1804.9	1096.1	764.2	1331.4			555.4
348-9	1979-80	2392.2	1539.0	1231.0	1561.4			939.8
Pack total	1979-80	2393.4	1539.9	1256.0	1561.4			
346-7	1980-81	754.6	596.2	359.5	754.6			
348-9	1980-81	841.7	639.9	400.9	841.7			
Pack total	1980-81	859.9	639.9	400.9	841.7			
Composite Pack Total	1978-81	2739.4	1782.6	648.1	1746.6			

[1] After Mohr (1947).

[2] After Harvey and Barbour (1965).

[3] After Dice and Clark (1953) and Tester and Siniff (1965).

[4] After Ables (1969).

[5] Blanks indicate inadequate number of locations to determine home range size.

Table 36. Geometric mean center of activity (GMCA), and mean activity radius for 22 collared wolves on the primary bison ranges of Wood Buffalo National Park, 1977 to 1981. GMCA indicated by UTM coordinates.

Wolf Number	Year	Winter GMCA	Number of Locations	Mean Activity Radius (km)	Summer GMCA	Number of Locations	Mean Activity Radius (km)	Winter to Summer Shift in GMCA (km)
U268	1977-78	4360E;64600N	8	14.9				
U270	1977-78	4245E;65315N	7	20.1	4125E;65490N	9	2.9	NNW - 20
U271	1977-78	4285E;65160N	9	8.4	4275E;65270N	11	8.4	NNW - 11
U215	1977-78	4576E;65970N	7	7.5	4490E;66070N	8	17.0	NW - 13
U259	1977-78	4285E;66475N	6	4.6	4225E;66435N	11	9.3	SW - 7
270	1978-79	4260E;65190N	7	10.5	4300E;65260N	7	9.0	NNE - 8
272	1978-79	4265E;65195N	6	10.8	4270E;65265N	10	5.8	N - 7
276	1978-79	4275E;65200N	5	11.5	4290E;65260N	11	6.4	NNE - 7
278	1978-79	4275E;65200N	5	11.5	4330E;65260N	14	7.6	NE - 9
281-2	1978-79	4230E;65195N	14	11.3	4315E;65260N	5	7.1	NE - 11
285-6	1978-79	4260E;65190N	7	10.5	4310E;65240N	15	7.2	NE - 7
269	1978-79	4575E;65940N	49	9.6	4495E;66005N	12	13.5	NW - 11
271	1978-79	4580E;65930N	49	8.4	4500E;66010N	13	12.7	NW - 12
275	1978-79	4555E;65940N	7	3.1				
279	1978-79	4580E;65950N	46	9.0	4505E;65845N	4	10.5	SW - 13
283-4	1978-79	4570E;65925N	6	7.4	4540E;65985N	19	14.6	NW - 7
346-7	1979-80	4620E;65890N	103	15.6	4445E;66105N	2	17.0	NNW - 28
348-9	1979-80	4620E;65850N	103	19.8	4435E;66130N	2	17.3	NNW - 33
323	1979-80	4560E;66195N	50	12.3	4585E;66300N	2	13.9	NNE - 11
346-7	1980-81	4505E;65990N	78	10.7				
348-9	1980-81	4505E;65995N	84	11.3				
323	1980-81	4605E;66115N	22	18.1				

Table 37. Size of winter and summer home ranges of 21 radio-collared wolves on primary ranges, Wood Buffalo National Park, as determined by polygon perimeter method (Mohr 1947) and mean activity radius (Tester and Siniff 1965).

Locality	Wolf Number	Year	Number Of Locations		Home Range Size (km^2)			
					Polygon Perimeter		Mean Activity Radius	
			Winter	Summer	Winter	Summer	Winter	Summer
Peace-Athabasca Delta	U270	1977-78	7	9	789.2	41.8	1268.6	26.4
	U271	1977-78	9	11	149.5	88.1	221.6	221.6
	U268	1977-78	7		707.4	697.1		
	270	1978-79	7	7	68.6	183.3	346.2	254.3
	272	1978-79	6	10	50.2	79.2	366.2	105.6
	276	1978-79	5	10	43.6	120.1	415.3	128.6
	278	1978-79	5	14	35.2	242.9	425.3	181.4
	281-2	1978-79	10	9	294.1	86.8	400.9	158.3
	285-6	1978-79	7	15	68.6	215.5	346.2	162.8
Hay Camp - Darough Creek Prairies	U215	1977-78	7	8	144.6	240.2	176.6	907.5
	269	1978-79	49	12	807.8	544.5	289.4	572.3
	271	1978-79	49	13	703.1	577.9	221.6	506.5
	279	1978-79	45	4	724.2	84.5	254.3	346.2
	283-4	1978-79	5	20	92.5	1136.3	171.9	669.3
	346-7	1979-80	103	2	1804.9		764.2	555.4
	348-9	1979-80	103	2	2393.2		1231.0	939.8
	346-7	1980-81	78	1	754.6		359.5	
	348-9	1980-81	84	1	859.8		400.9	
Salt Plains	U259	1977-78	6	11	90.0	343.0	66.4	271.6
	323	1979-80	50	2	544.9		490.6	606.7
	323	1980-81	23				895.7	

section. An exception occurred in 1979-1980, when the winter mean activity radius of wolf no. 348-9, and the Hornaday River pack, was approximately three times that of pack members in other winters (Table 37), a result of exploratory movements in January and February into the upper Slave River Lowlands and the Peace-Athabasca Delta.

A comparison of home range sizes north and south of the Peace River showed that with the polygon-perimeter method, mean winter home range size of wolves in Area I was marginally larger than that in the Peace-Athabasca Delta, but was somewhat smaller than that calculated by activity radii (Table 36). These differences were primarily due to the configuration of winter home ranges in the Peace-Athabasca Delta in 1978-1979, as drawn by joining a small number of perimeter points (Table 37). Summer home range sizes in both cases were considerably larger (t - test, $p = .007$) in Area I than in the Peace-Athabasca Delta, and may have been a result of the year-round availability of bison in predictable areas in the Delta as compared to more scattered bison in the northern area.

Pack separation in summer was temporary, and although packs were most often split into smaller groups (Table 38), pack members remained associated throughout the summer. With the exception of female no. 270, all collared wolves in the Lake Claire pack were located at least once with another collared pack member during the summer. Similarly, members of the Hornaday River pack maintained contact during the summer, and the apparent greater degree of separation between collared wolves was most likely a result of the lesser number of collared individuals (Figure 37).

Because wolves were located by radio-tracking less regularly in summer than in winter, it was generally not possible to pinpoint geographical centers of activity as carefully in summer as compared to the winter. However, ground observations in areas of habitual summer use, as determined by aerial radio-tracking (Figure 38) made it possible to locate denning and rendezvous sites.

Fidelity of the Hornaday River pack to certain portions of its winter range was determined for each summer 1978 to 1981, as well as for the three winter periods from 1978 to 1981. Observations of the home range occupied each year indicated most portions of the home range were used only occasionally each winter, but some portions were consistently heavily utilized (Figures 39 and 40; see also Table 39). The latter areas consisted primarily of meadows (Figure 41), which also comprised prime winter habitat for bison, but were not always occupied by bison. In this situation, bison herds in the north, when compared to those in the Delta, are probably shifting targets, their precise location not always predictable.

Analysis of winter home range use by the Hornaday River pack for two or more radiolocations per 6.25 km^2 (Figure 39) showed that 60% of locations were recorded in 36% of the area occupied in 1978-1979, 51% in 32% in 1979-1980, 70% in 46% in 1980-1981, and 79% in 50% of the area occupied in winters 1978-1979 to 1980-1981 combined. Similarly, the proportions of locations within the area circumscribed by the mean activity radius, or standard diameter (Figure 42, Table 35) closely resembled the theoretical 68.36% of all locations in each

Table 38. Cohesion and splitting of wolf packs in winter (W) and summer (S) on primary bison ranges, Wood Buffalo National Park, 1977-1978 to 1980-1981, as determined by occurrences of smaller radio-collared groups.

			Number of Smaller Groups											
			Entire Pack[1]		2		3		4		5		Total	
Pack	Year	Number of Collared Wolves	W	S	W	S	W	S	W	S	W	S	W	S
Lake Claire	1977-78	2-3	0	0	5	14	5	0					10	14
	1978-79	2-6	14	3	0	3	0	5	0	3	0	1	14	15
Hornaday River	1977-78	2	3	0	2	0							5	
	1978-79	2-4	41	2	7	7	3	5					51	14
	1979-80	2	95	1	8	1							103	2
	1980-81	2	73	1	9								82	1

[1] All radio-collars present.

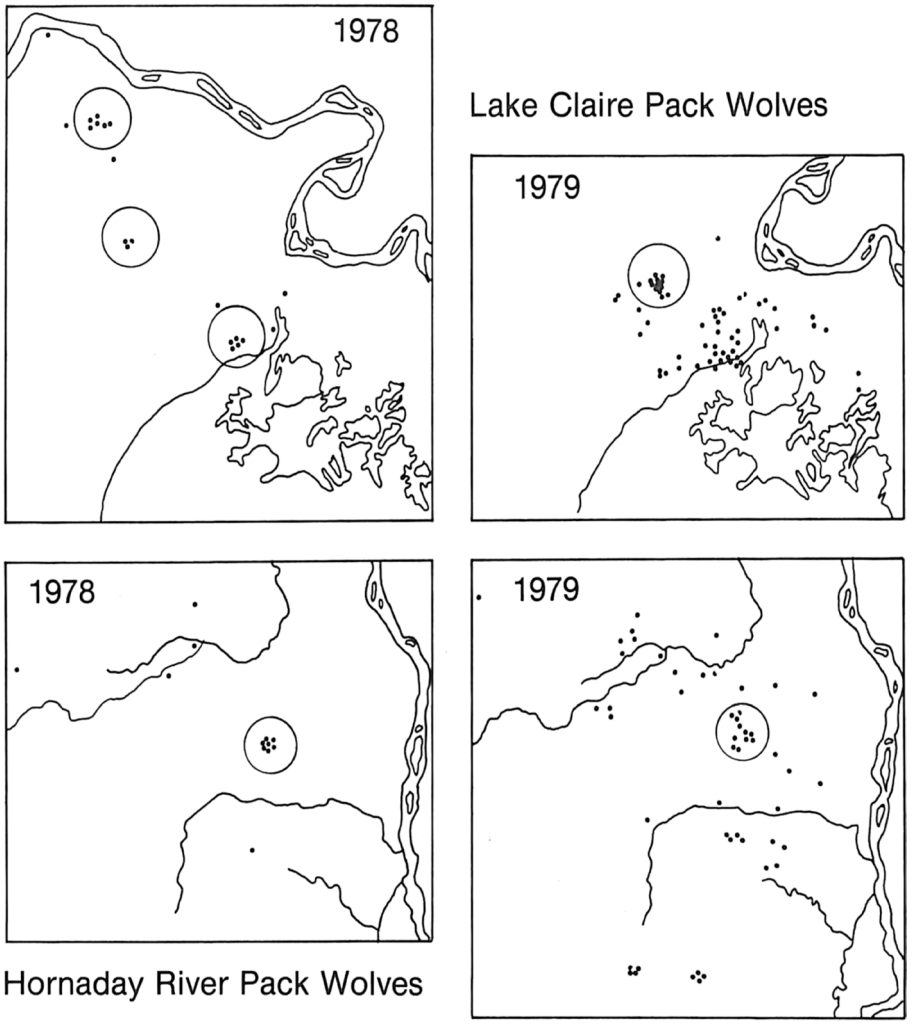


Figure 38. Geographical distribution of radiolocations for the Lake Claire and Hornaday River wolf packs; summers 1978-1979, showing areas of concentrated activities.

winter (Dice and Clark 1953) and thus was considered an adequate definition of the area of concentrated use (Table 40).

Comparisons of our home range data with those of other studies could be made only for size calculations based on the conventional polygon-perimeter method. On this basis, annual home range sizes for packs in winter in Wood Buffalo National Park were considerably larger than those reported for wolves preying on deer in Minnesota and Ontario (Mech and Frenzel 1971, Kolenosky 1972, Van Ballenberghe et al. 1975,

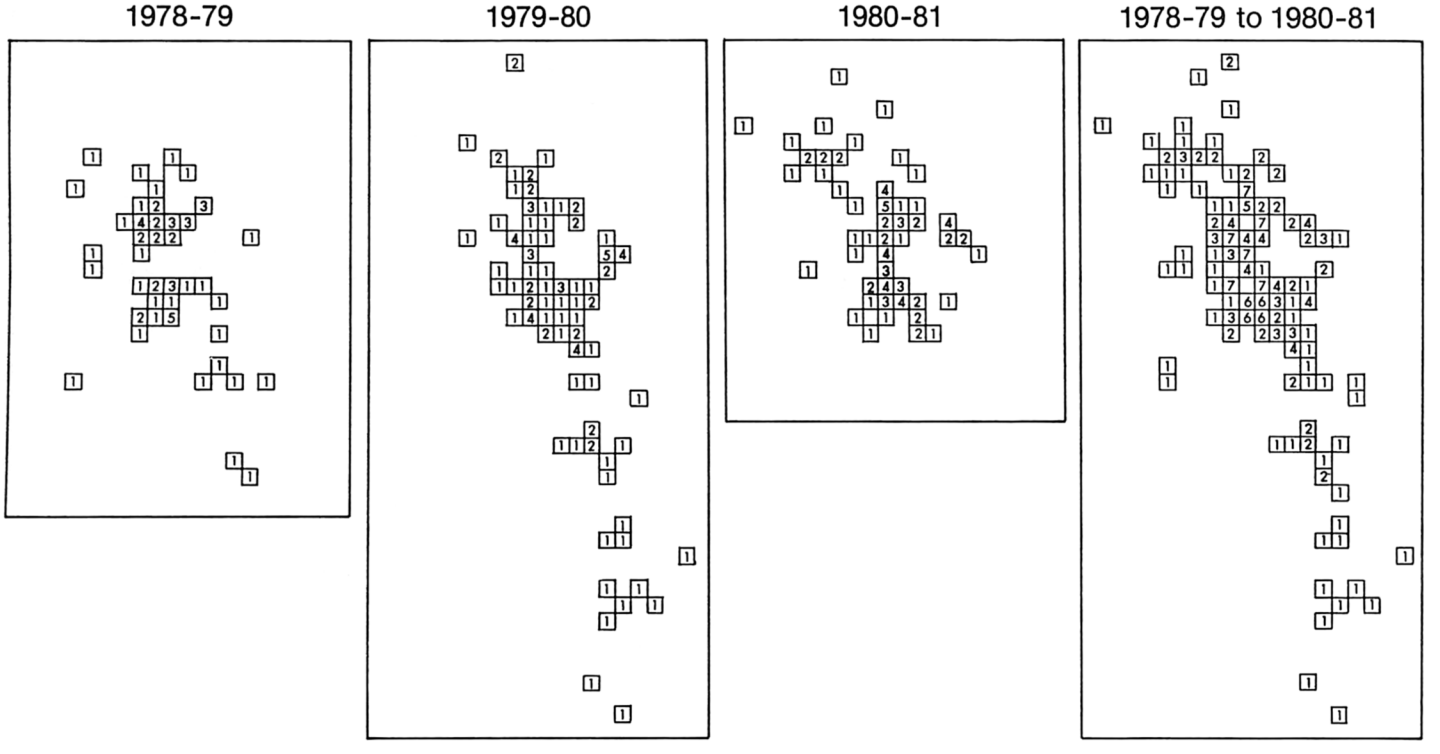


Figure 39. Utilization of winter home-ranges of the Hornaday River pack as determined from the number of radiolocations in 6.25 km^2 units.

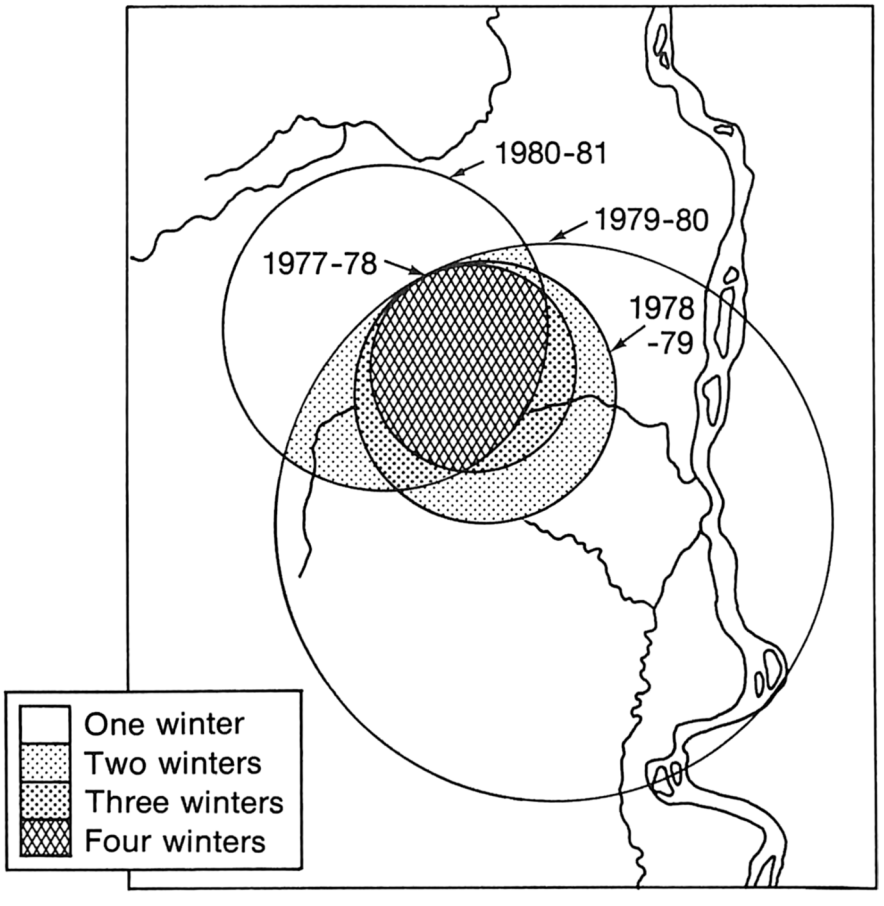


Figure 40. Overlap in mean activity radii in winter for the Hornaday River pack, winters 1977 to 1981.

Fritts and Mech 1981) for wolves and moose in Isle Royale (Peterson 1977), and wolves and elk in Manitoba (Carbyn 1980).

Fritts and Mech (1981) calculated the composite annual home range of eight packs over several consecutive years and found that ranges varied from 195 to 555 km^2. They reported no geographical shifts from winter to summer, and packs apparently remained cohesive in summer. The composite home range of the Hornaday River pack was 2,740 km^2 during winters 1977-1978 to 1980-1981. The dispersal of pack members into separate, although probably temporary groups made it difficult to define the pack's summer range, but inclusion of location points for all collared wolves in summer increased the size of the year-round home range to over 3,000 km^2.

Table 39. Home range use by the Hornaday River pack, as determined by radiolocations in 6.25 km^2 units.

Year	Number of 6.25 Km^2 Units in Home Range	Locations Per Square Unit									
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1978-1979	39	25	7	5	1	1					
1978-1979	69	47	14	3	4	1					
1980-1981	48	26	12	4	5	1					
1978-1981	107	54	21	7	9	5	4	5	1		1

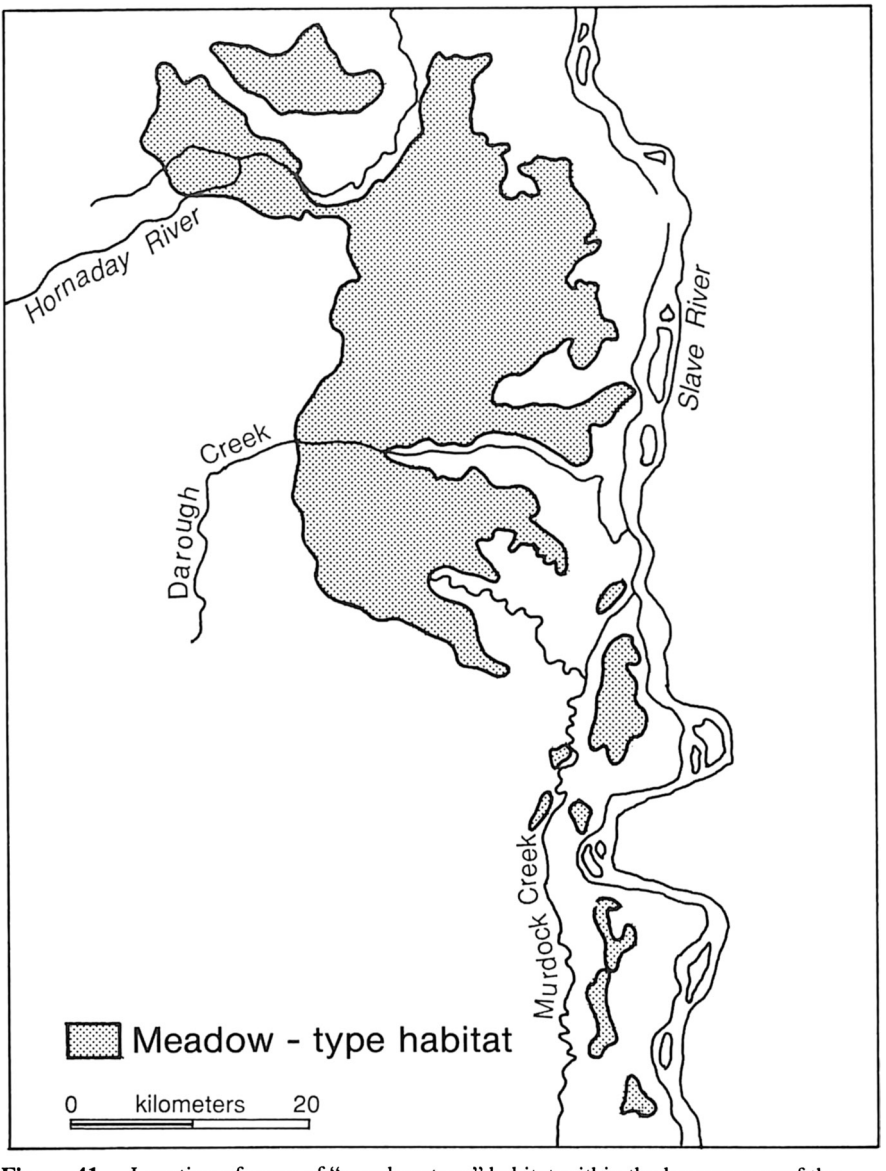


Figure 41. Location of areas of "meadow-type" habitat within the home range of the Hornaday River pack.

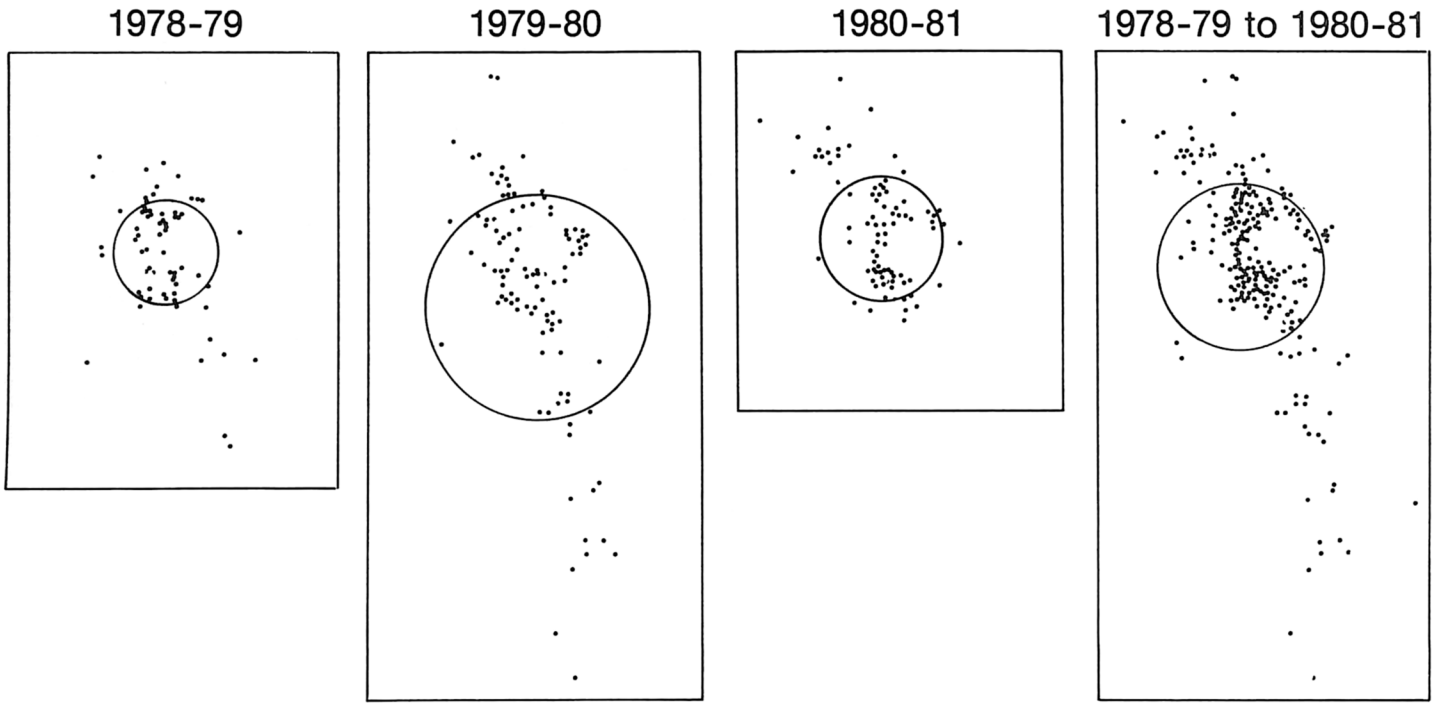


Figure 42. Distribution radiolocations relative to mean activity radii of the Hornaday River pack, 1978-1981.

Table 40. Theoretical and actual number of locations of the Hornaday River Pack[1] within the mean activity radius in winter 1978-1979 to 1980-1981.

Year	Geometric Mean Activity Center	Total Number Locations	Mean Activity Radius (km)	Number of Locations	
				Observed	Expected[2]
1978-79	4580mE;65950mN	65	9.1	39	44
1979-80	4620mE;65850mN	103	20.0	72	70
1980-81	4560mE;65970mN	84	11.3	54	57
Composite					
1978-81	4590mE;65915mN	252	14.6	165	172

[1] Includes locations of all pack members.

[2] Expected number of locations based on 68.26% proportion within standard diameter (Dice and Clark, 1953).

Our data on home range size in relation to five-point interval locations suggested that in 1979 the winter home range for the Lake Claire pack was probably not adequately defined due to a small number of locations. Summer locations indicated differences in home range size between pack members, both in 1978 and 1979, although it was not possible to follow into the next winter any dispersing wolves such as was the case with one male (no. U270).

Home range size appeared to be adequately defined for the Hornaday River pack at approximately 800 km^2 in 1978-1979, 1979-1980, and 1980-1981, but dispersal of wolves in summer, as well as an apparent range expansion in 1979-1980, resulted in a much larger total area. The latter event appeared to have been a temporary incursion into areas occupied by adjacent wolf packs, because the Hornaday River pack primarily occupied its pre-1980 home range again in 1980-1981. Rapid changes in home range were interpreted as shifts by packs into adjacent "territories" (Carbyn 1980), which may have been the case for the Hornaday River pack in 1980, because collared pack size decreased from 14 to 7 between April and November 1980, possibly as a result of a more permanent split in the pack.

Geographical shifts from winter to summer home ranges were evident in all cases. These shifts appeared to be a result of bison movements northwest away from Lake Claire, and northwest out of the Hay Camp-Darough Creek prairies into the Alberta Plateau, and may be similar to observations of wolves moving northward with caribou herds which are travelling from winter to summer areas (P. Clarkson, pers. comm.). Differences in summer home range size between members of the Lake Claire and Hornaday River packs may have been a reflection of the relative distance that bison move in each of these localities from winter to summer ranges. Home range sizes for the Hornaday River pack wolves in summer were considerably larger than those of the Lake Claire pack; however, mean distances between consecutive locations (Table 41) were not, suggesting that wolves in both areas travelled similar distances, but the Hornaday River pack wolves travelled farther afield in response to greater bison movements. This observation again supports the "foraging" theory of different foraging ranges in Areas I and II. Density calculations were based on the population estimates of four packs north of the river and six packs south. Primary ranges north were set at 4,000 km^2 and south at 5,000 km^2 in winter when the Delta water system is frozen. If the wolf population for all major primary areas varied from 80 to 220 (including those wolf packs at the fringes whose movements are largely within secondary ranges) the density figures in Area I ranged from a low of one wolf per 125 km^2 to a high of one wolf per 46 km^2. Comparable data for Area II was a low of one wolf per 104 km^2 to a high of one wolf per 38 km^2. The highest densities recorded prior to freeze-up in the fall, when pack sizes are largest, and during bison migration reached levels of one wolf per 2.56 km^2.

Table 41. Mean straight-line distances between locations of radio-collared wolves in the Lake Claire and Hornaday River packs, Wood Buffalo National Park; summer 1979 (number of locations in brackets).

Pack	Wolf Number	Mean Number of Days Between Locations	Mean Distance (Km) Between Locations
Lake Claire	270	13 (5)	12.7
	272	13 (8)	13.1
	276	12 (9)	15.3
	278	14 (11)	16.9
	281-2	10 (3)	17.9
	285-6	13 (12)	18.2
MEAN		12 (48)	15.9
Hornaday River	269	11	17.0
	271	11 (10)	13.1
	279	6 (1)	6.8
	283-4	10 (15)	24.7
MEAN		10 (35)	15.4

v) Territoriality and intraspecific relations

The concept of territoriality has been applied to wolves by various authors but not until the 1970s. Radiotelemetry was a means by which more precise information on the spatial-temporal relationships between wolf packs could be studied.

Burt (1943) first defined home ranges although the concept had been discussed earlier in the 1920s and 1930s by ornithologists. Only since the 1980s have the statistical properties of some commonly used models been tested (Bekoff and Mech 1984, Boulanger and White 1990). Burt (1943) defined home ranges as "areas over which an animal normally travels in search of food", whereas territories were considered that part of the home range defended against conspecifics. In some cases (Mech 1977, Peterson 1977), defence of space, i.e., physical contact between packs causing death of wolves has been observed. Ballard et al. (1981) reported that pack territories in central Alaska were essentially non-overlapping and defended, although intrusions into neighbouring territories often occurred when the home pack was absent from that portion of the area. Other less overt forms of "territorial behaviour" such as scent marking (Peters and Mech 1975), howling (Harrington and Mech 1979), and avoidance (Peterson 1977) have been documented.

The question of whether territoriality exists among wolf packs preying on clumped and mobile prey species such as caribou and bison, has only been partially answered. Stephenson and James (1978) implied that wolves travelled with migrating caribou into areas of winter concentration; however, no observations of intraspecific tolerance or intolerance were noted. Studies currently in progress in the Arctic indicate that in late winter, wolves tend to travel hundreds of kilometres with caribou toward their calving grounds (P. Clarkson, pers. comm.). Van Camp (1987c) documented considerable overlap in the territories of what he assumed were three neighbouring packs that preyed on approximately 300 bison in the Slave River Lowlands in late winter 1976-1977.

Home range overlap in our study area (Figure 43) was documented for two neighbouring collared packs during winters 1979-1980 and 1980-1981, and for two collared packs in late summer 1979. On 1 February 1980, a pack of seven unmarked wolves (Salt River pack) was resting on the bank of the Salt River within the home range of the Hornaday River pack, and they later killed a bison south of the river. The pack remained in the vicinity of the kill for a week. Three of its members were captured and collared. On 24 February the Hornaday River pack attacked and killed two of the collared wolves, and the pack was fragmented as a result. The remaining collared wolf subsequently returned to the kill, and later in March spent 13 consecutive days near another bison carcass at the edge of the Hornaday River pack's range. This wolf re-established only temporary ties with other surviving Salt River pack members. On three occasions it was located with other wolves, each time outside the Hornaday River pack's winter range. During this time, it was recovering from a trap-inflicted injury to one of its feet, and apparently was unable to travel with the pack.

In 1980-1981, a group of three wolves, including the remaining collared Salt River pack member and a former member of the Hornaday River pack, spent approximately 50% of their time within the boundaries of the Hornaday River pack's winter range (Figure 43). The Hornaday River pack wolf was believed to have been a dominant male in 1978-1979, and its knowledge of the Hornaday River pack's winter range was suspected from the manner in which these three wolves occupied the area. Association between unrelated wolves has been shown to occur in northwestern Minnesota (Fritts and Mech 1981), where in an expanding wolf population, such events commonly led to the formation of new packs.

In late October 1979, the Lake Claire pack was located in the area occupied by the Baril Lake pack the previous winter. As the Baril Lake pack was not under surveillance at this time, it is not known whether the area had already been vacated by the pack, the pack was in another part of its range, or the Lake Claire pack had displaced the Baril Lake pack. Judging from ground observations in October 1990 and 1991, it is likely that tolerance between packs existed.

Determination of pack affiliation of wolves was not always possible; however, a number of instances occurred where wolves not normally associated with the Hornaday River pack were found within the boundaries of the Hornaday River pack's composite home range. These intrusions, or potential overlap of home

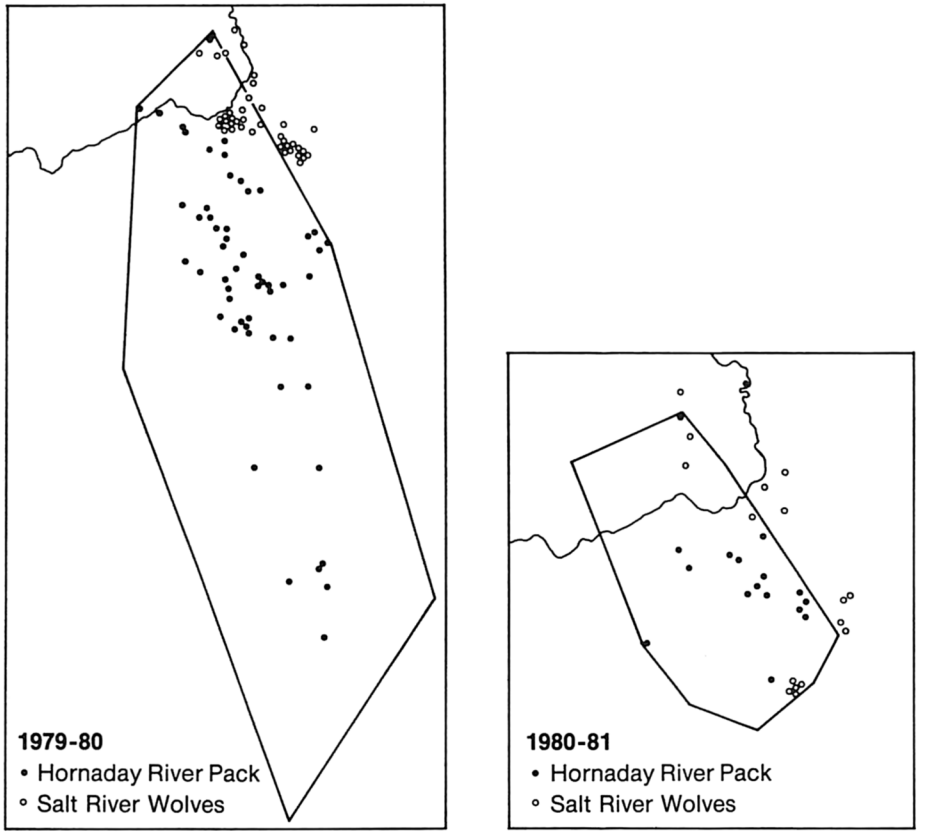


Figure 43. Location of Salt River pack wolves within and adjacent to the annual winter home range of the Hornaday River pack 1979-1981.

ranges, may have occurred as a result of annual, seasonal or even shorter excursions by the Hornaday River pack away from portions of its home range. Similar observations were made in October 1990 when members of a large pack (26 animals) were seen hunting in an area occupied by members of a different pack (14 members) and where members of the smaller pack pursued the intruders.

The Hornaday River pack showed fidelity to certain parts of its home range (Figure 40). Approximately 65% of all pack locations between 1978-1979 and 1980-1981 were recorded within a 670 km^2 circle bounding the mean activity radius for those years (Table 40); no packs other than the one of questionable status (Darough Creek pack) were ever located within its boundaries. Movements of the Hornaday River pack of more than 25 km, away from the periphery of this home range core, occurred twice in midwinter 1980, when the pack travelled south into areas known to have contained at least two other packs the previous year. In both instances the pack made a kill. In late March 1980, the pack travelled 18 km north of its home range core and visited a den site thought to have been occupied by the Salt River pack the previous summer.

Tenure of home ranges by wolves within Wood Buffalo National Park are influenced by the mobile nature of its major prey. This is particularly true in fall and winter, when prey species in any one area are reduced, clumped, or moving from summer to winter ranges.

In the case of the intensively studied Hornaday River pack, we suspect that it maintained a home range core exclusive of other packs, but frequently ventured into areas outside this core. Wolf movements in Wood Buffalo National Park may be primarily food motivated, as was the case for the Salt River pack in February 1980 (few bison were recorded on surveys north of the Salt River in winter 1979-1980). The Hornaday River pack most likely ventured into "foreign" terrain in response to bison movements. In the Delta, drying has reduced alternate food sources for wolves (muskrat, beaver, waterfowl), and concentrated bison herds, thereby changing the general regime of food availability to wolf packs in this area.

2. *Wolves Killed by Humans*

A. *Introduction*

Wolf control programs from 1935 to the late 1960s were designed to reduce wolf predation on caribou, moose and bison. During these programs, and subsequently, wolf trapping and hunting was a legal means for native residents to obtain fur for commercial purposes.

Wolf fur is widely used for garments. Wolf hair tends to be brittle, but does not mat or hold frost, therefore parka trim is often made from wolf pelts. Trappers in the Park obtain wolves through opportunistic trapping and some wolves are illegally hunted by running them down on snow machines. Those who do so show little mercy toward a predator that is seen to cruelly maul and kill bison year round.

B. *Methods*

Wood Buffalo National Park has kept records of the number of wolves officially registered as having been killed each winter. These records are kept on file and were summarized up to 1976 (Church 1976, Milne 1989).

C. *Results and Discussion*

Hunting and trapping of wolves in Wood Buffalo National Park has been carried on before and since the establishment of the Park; fur harvest figures from 1950 to 1987 are shown in Figure 44 (Milne 1989). Prior to 1975, these figures were considered incomplete, because they reflected only wolves sold in the Park area; pelts sold in southern markets went largely unrecorded (Church 1976). As well, until 1975 the Northwest Territories government offered a forty dollar bounty on wolves. Before 1970, this amount was greater than the dealer's price for the pelt, therefore, it seems likely that many Park wolves killed in Alberta were taken into the Northwest Territories for bounty payment.

It is also possible that in the past, some Alberta park trappers may have submitted wolf pelts to the N.W.T. Wildlife Service in Fort Smith, by way of Northwest Territories non-park trappers. The Northwest Territories government did not collect fur tax, and usually paid the trapper on the spot; Park wolves would then go unrecorded. This practice, however did not seem to have occurred often. A certain number of pelts are bartered locally or used privately for garments, but this appears to account for a minimal number of wolf pelts.

Wolf harvest figures since 1975 have been determined by examination of yearly written declarations submitted by trappers at the time of permit renewal, as well as records of local fur buyers and both the N.W.T. Department of Renewable Resources and Alberta Fish and Wildlife. Pelts taken in the Northwest Territories' section of the Park are sent by Renewable Resources to fur auction houses in Edmonton, (Alberta) and the numbers recorded and sent to Park headquarters. The Park Warden Service collects a fur tax on pelts taken in the Alberta section as a favour to the Alberta Fish and Wildlife, which in turn provides records for all pelts sold in Edmonton. In addition, all furs leaving Fort Smith (Northwest Territories) require an export permit for sale in Alberta; these are also dispensed by the Warden Service.

Known records of wolf harvest and population estimates indicated that trapping of wolves in the Park since 1976 has continued to be relatively light. It is possible that a large number of wolves may have been taken in the years 1973-1974 and 1974-1975, but the wolf population was higher during those years than at present. High fur prices in the mid 1980s and increased illegal use of snow machines at the time, particularly in the open Peace-Athabasca Delta region, where access is much better than in areas north of the Peace River, may have made wolves a more desirable fur species. The fur harvest records however, do not bear this out.

Although some trappers have been successful at trapping wolves in and around the periphery of the Park (one trapper snared more than 20 wolves adjacent to the Salt River between 1978 and 1981), most do not actively trap wolves because they are

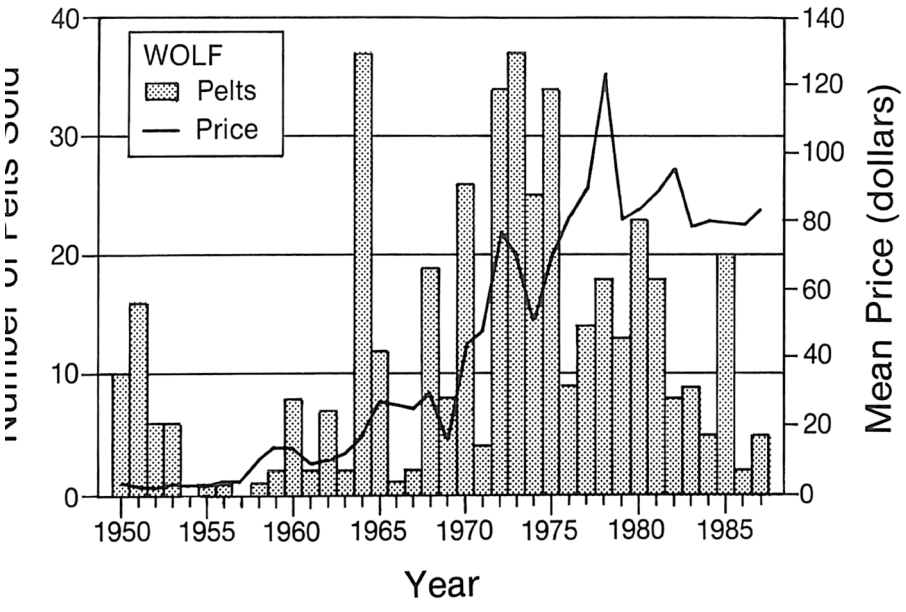


Figure 44. Wolf pelt harvest in Wood Buffalo National Park, 1950-1987.

difficult to catch (Soper 1945), and prices for wolf pelts were relatively low in the 1980s when compared to fine furs such as lynx and fox. In some cases, native trappers refuse to trap or kill wolves because of traditional beliefs (S. Flett, pers. comm.).

Four radio-collared wolves were killed in snares between 1977-1978 and 1980-1981. Collar returns (small sample size) indicated that trapping mortality for collared wolves did not exceed 8% in any year, assuming other sources of mortality occurred in the observed magnitude based on collar recovery.

3. *Canid Interactions*

Five species of canids have been recorded for the Park. Two species, the gray fox (*Vulpes cinereoargenteus*) and arctic fox (*Alopex lagopus*) are extralimital, with the occurrence of the gray fox being a single most unusual record (Moore 1952) in that the nearest location of the range of the species is several thousands of kilometres removed. Arctic fox have occasionally been seen in the Park (Soper 1942), and probably follow cyclical events within their main ranges to the northeast of the Park. From 1935 to 1944, five arctic foxes had been reported for Wood Buffalo National Park (Soper 1945).

Red foxes (*Vulpes vulpes*), and their colour variants, were common in the Park from the early 1980s to the present. Numbers have fluctuated over the years. A review of their abundance indicated that the species was common in the early 1930s, less so in the early 1970s, and was so common in the Peace-Athabasca Delta during

1985-1990 that it could be encountered daily in all seasons of the year. Reduction in trapping pressures may partly account for increased sightings. In 1990, we found red foxes denning within 1 km of a wolf den and one rendezvous site.

Coyotes (*Canis latrans*), on the other hand, were virtually absent from the Delta during the 1980s. According to Park records, coyotes increased in the Wood Buffalo Park region when the species spread northwards as a result of the opening of agricultural areas in Alberta in the 1890s. Preble (1908) cited records of incidental occurrences in northern Alberta at the turn of the century. Soper (1942) noted that coyotes in the Park increased considerably from 1890-1930, a period when he also noted that wolf numbers were lower than in later years. During subsequent visits to the Park, he observed an increase in wolf numbers and a marked decrease in coyote sign (Soper 1945).

The average number of coyotes trapped from 1935 to 1945 was only 18% of the number killed in the winter 1934/35 (Church 1976). Coyotes increased in the 1960s and remained abundant until the mid 1970s. Native trappers commonly reported seeing "many coyotes" at wolf kills, and a biologist surveying the Delta for the International Biological Program reported seeing abundant sign (Gunson 1969). In contrast, during 116 days living and working on the Delta, Carbyn saw only two coyotes from 1985 to 1991. This superficial historical overview suggests an approximately inverse relationship between the abundance of wolves and coyotes. The individual or combined impact of wolves and coyotes on red foxes is unclear; certainly, foxes are often seen scavenging on wolf kills. It is obvious that the three canids interact in some dynamic manner. The details of these interactions require further study.

4. *Ravens*

One of the most common birds in the Peace-Athabasca Delta is the raven (*Corvus corax*). Its presence is closely linked with wolf predation. In June 1990, over 80 ravens were seen in association with a kill of a calf (count of exact number was not possible). Around 0600 hours on that occasion a cow defended her dead calf against seven wolves for about 2 hours. During that time ravens constantly attempted to scavenge, but were interrupted by the intense interactions between the cow and the wolves. Later that same day, another kill was found (again a calf), and not one raven was seen at that kill. During summer, ravens frequently appear on the scene when wolves attempt to kill calves. They leave the area if kills are unsuccessful.

The dynamics between these scavengers and their environment need further study. Interesting observations are currently being made on ravens and wolves in the Yukon Territory (R. Hayes, pers. comm.). An observer, C. Promberger (Univ. of Munich, unpubl. data) found that prey biomass consumed by scavengers is inversely related to pack size, i.e., with fewer wolves per pack more prey biomass is consumed by scavengers (Hayes 1991). In that study it was found that ravens can account for the consumption of large amounts of meat, amounting to possibly as much as 45 kg per carcass (R. Hayes, pers. comm.).

VII Predator and Prey Relationships

1. *Winter Predation*

A. *Introduction*

Wolf:bison ratios in the 20-year period (1971-1991) have undergone wide fluctuations. The major trend has been a significant decline in the bison herd and general increases in wolf numbers. In this chapter we summarize some of the parameters relating to the mechanics of this interaction and evaluate the consequences through preliminary modelling exercises.

We based the conclusions about wolf predation rates and prey selection primarily on winter observations of the Hornaday River pack, a group of wolves occupying most of the primary bison ranges north of the Peace River, and on summer observations of packs in the Sweetgrass area south of the Peace River. The impact of predation by wolves was evaluated by comparing the proportion of bison killed each winter and summer to the bison recruitment. We calculated prey availability from the annual midwinter total count conducted by Park wardens and evaluated early summer calf production, summer mortality and yearly recruitment by examining data obtained from classified counts.

The number of bison killed by wolves in winter was extrapolated from data collected by radio-tracking the Hornaday River pack. Predation rates over 180 days (November-April) were then calculated for the total wolf population on the primary bison ranges. We calculated summer kill rates using field observations from 1985 to 1991, relative biomass consumption from scats collected during 1977 to 1980, and known average daily food requirements of wolves (Mech 1977) extrapolated over 180 days (May-October), and converted to number of adult bison and calves killed in specified periods of time.

Models were constructed to describe the impact of wolf predation over the entire primary bison ranges. Observed values for calf survival and calculated values for adult mortality at various intervals throughout the year were used for these models, based on 1978 to 1991 studies.

B. *Methods*

The Hornaday River pack was relocated daily from aircraft from 19 February to 6 April 1979, from 3-31 December 1979, 18 January to 7 April 1980, 9-31 December 1980, and 21 January to 14 April 1981. By spacing intensive monitoring periods over time it was possible to compare early winter predation rates (large packs, less snow) with late winter (smaller packs, more snow accumulation, and possibly food-stressed prey). All pack locations, kill sites, travel routes and chase sequences were marked on 1:54,000 aerial photographs. Concurrent ground tracking on snow machines or skis was carried out to examine wolf-killed prey. In addition to kills examined from radio-collared wolves, data was provided by the kills examined by Park wardens from 1971 to 1981.

Ground examination included checking snow conditions and investigating evidence of the length of the chase. Lower jaws and femurs were collected to determine age and condition of bison. Kills were not examined until after the wolves had voluntary abandoned them. If not completely consumed, kills were periodically re-examined to determine the frequency of re-visitation by wolves.

Biomass calculations were based on live weights of bison (H. Reynolds, pers. comm.); it was assumed that 80% of any carcass was edible (Pimlott 1967, Mills 1990). Mean pack size was used to determine prey biomass consumed per wolf per day. Incisors were sectioned and decalcified (Sergeant and Pimlott 1959) and cementum layers counted as an estimate of age (Armstrong 1965). Femurs were analyzed for fat content (Verme and Holland 1973) to determine extent of malnutrition.

Age structure of bison in the Park was determined from roundup figures at Hay Camp (Novakowski and Choquette 1963) and Sweetgrass (Novakowski and Choquette 1964), the 1971 field slaughter (Currier 1971), and early winter calf surveys from 1978 to 1980. Age structure of wolf-killed bison was compared to the estimated age structure of the population, and differences were evaluated by means of Chi-square analysis.

C. *Results And Discussion*

i) Predation rates and prey utilization

During eight periods of intensive aerial tracking of the Hornaday River pack in winter (total 285 days), the pack killed 40 bison and two moose, or an average of one animal every 6.8 days (Table 42). Data on prey consumption indicated a high degree of utilization of carcasses by the Hornaday River pack (Table 43). In winter, these wolves normally consumed a bison calf entirely within one session and did not revisit remains of calf carcasses. Adult bison were usually not totally consumed before being first abandoned by the pack, but in all cases were completely utilized within a month of being killed (Table 43).

The Hornaday River pack spent an average of 2.4 days at each adult bison carcass after first killing it (Table 43). Our data is similar to that of Fuller and Keith

Table 42. Predation rates and prey consumption by the Hornaday River pack in Wood Buffalo National Park; 1978-1979 to 1980-1981.

			PREY KILLED AND CONSUMED[2]								
			Adults[1]								
Year	Intensive monitoring period	# of days	Males	Females	Calves	Yrlgs	Total	No. of prey killed/ day	Mean pack size	Prey biomass/ pack/day[4] (kg)	Prey biomass/ wolf/day[4] (kg)
1978-79	12/02/79-18/02/79 (MW)	17	2	-	-	-	2	0.12	10	64.0	6.4
	01/03/79-31/03/79 (LW)	31	2	2	-	-	4	0.13	10	61.0	6.1
TOTAL		**48**	**4**	**2**	**-**	**-**	**6**	**0.13**	**10**	**62.0**	**6.2**
1979-80	14/11/79-27/12/79 (EW)	44	-	1	4	2	7	0.16	12	30.5	2.5
	18/01/80-29/02/80 (MW)	43	2[3]	3[3]	3	1	9	0.21	13	61.2	4.7
	01/03/80-07/04/80 (LW)	38	-	2	4	-	6	0.16	10	35.4	3.5
TOTAL		**125**	**2**	**6**	**11**	**3**	**22**	**0.18**	**12**	**40.3**	**3.4**
1980-81	09/12/80-21/12/89 (EW)	23	-	2	-	-	2	0.09	7	35.0	5.0
	15/01/81-28/02/81 (EW)	44	1	2	2	-	5	0.11	8	36.8	4.6
	01/03/81-14/04/81 (LW)	45	1	2	4	-	7	0.15	8	41.6	5.2
TOTAL		**112**	**2**	**6**	**6**	**-**	**14**	**0.12**	**8**	**38.4**	**4.8**
Combined winter	Early Winter (EW)	67	-	3	4	2	9	0.13	10	32.0	3.2
	Midwinter (MW)	104	5[3]	5[3]	5	1	16	0.15	10	51.3	5.1
	Late winter (LW)	114	3	6	8	-	17	0.15	9	44.9	5.0
TOTAL		**285**	**8**	**14**	**17**	**3**	**42**	**0.15**	**10**	**44.2**	**4.3**

[1] Bison older than two years.

[2] Assumes 100% consumption by Hornaday River pack only.

[3] Total includes one adult male moose and one adult female moose.

[4] Based on 80% edibility (Mills 1990; Pimlott 1967) of 625 kg for adult male bison, 470 kg for adult female bison, 190 kg for bison calves, 300 kg for bison yearling, 500 kg for adult male moose, and 350 kg for adult female moose.

Table 43. Mean prey utilization rates[2] for the Hornaday River pack in Wood Buffalo National Park; winters 1978-1979 to 1980-1981.

			ESTIMATED AMOUNT CONSUMED				
Date of kill	Sex	Age[1]	First examination[3]	Second examination[3]	Third examination[3]	No. of days pack at kill	No. subsequent relocations at kill[5]
19/01/79	M	6	2 (1)	4 (43)		1[4]	-[7]
12/02/79	M	9	3 (9)	4 (35)		3	2 (3)
24/12/79	M	7	2 (3)	3 (7)	4 (12)	2	1 (1)
12/03/79	F	7	2 (4)	4 (23)		4	1 (3)
20/03/79	M	10	4 (21)			1	1 (2)
28/03/79	F	11	4 (8)			2	-
31/03/79	M	10	3 (5)	4 (37)		3	-
11/04/79	F	12	4 (2)			2	-
21/04/79	F	-	1 (1)			-[4]	-
14/11/79	F	YLG	4 (2)			-	0
23/11/79	-	YOY	4 (12)			1	0
29/11/79	F	9	4 (7)			2	0
15/12/79	F	YLG	4 (5)			1	0
17/12/79	-[7]	YOY	4 (3)			1	0
22/12/79	-	YLG	4 (26)			1	0
27/12/79	-	YOY	4 (3)			2	0
19/01/80	M	17	4 (26)			2	0
24/01/80	F	9	4 (7)			3	1 (1)
30/01/80	F[6]	4	3 (3)			1	0
31/01/80	F	12	4 (3)			2	0
04/02/80	M[6]	6	4 (3)			2	1 (1)
13/02/80	M	YLG	4 (3)			1	0
17/02/80	-	YOY	4 (10)			1	0
20/02/80	-	YOY	4 (4)			1	0
23/02/80	-	YOY	4 (2)			1	0
02/03/80	M	YOY	3 (2)	4 (8)		2	0

Table 43. Continued.

Date of kill	Sex	Age[1]	ESTIMATED AMOUNT CONSUMED			No. of days pack at kill	No. subsequent relocations at kill[5]
			First examination[3]	Second examination[3]	Third examination[3]		
10/03/80	-	YOY	4 (4)			1	0
13/03/80	-	YOY	4 (1)			1	0
23/03/80	F	9	4 (7)			3	0
27/03/80	F	8	4 (3)			2	0
06/04/80	-	YOY	-			-	0
09/12/80	F	14	4 (6)			2	0
28/12/80	F	17	4 (2)			3	1 (1)
15/01/81	-	YOY	4 (9)			1	0
20/01/81	F	8	4 (4)			2	0
04/02/81	M	15	4 (11)			3	1 (1)
15/02/81	F	8	2 (1)	4 (20)		4	0
25/02/81	-	YOY	4 (6)			1	0
02/03/81	-	YOY	4 (1)			1	0
08/03/81	-	YOY	4 (1)			1	0
13/03/81	F	3	4 (4)			2	0
19/03/81	-	YOY	4 (1)			1	0
24/03/81	F	12	2 (1)	4 (11)		24	1 (1)
28/03/81	M	16	3 (3)	4 (16)		2	0
13/08/81	-	YOY	4 (1)			1	0

[1] Age of adult bison determined by sectioning of incisors.

[2] Percent of edible portions consumed: 1 = 0-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%.

[3] Figures in brackets are number of days between date of examination and date of kill.

[4] Wolves prematurely left kill due to human disturbance.

[5] Radiolocations do not accurately reflect follow-up utilization of bison kills; figures in brackets are number of days pack was known to revisit former kills.

[6] Adults moose.

[7] No data available.

(1980) where packs of 9-11 wolves remained at kills of adult moose an average 2.5 days and at calf kills an average of 1.5 days. Carcass utilization in that study was also complete. Although other wolves (singles and pairs), as well as smaller scavengers such as foxes and ravens were observed to feed on bison carcasses, wolves in the Hornaday River pack were the major consumers of the bison they killed.

Meat consumed per wolf per day varied from 2.5 kg in early winter 1979-1980 to 6.4 kg in midwinter 1978-1979 (Table 42). This study indicated that over three winters each wolf in the Hornaday River pack consumed an average 4.3 kg per day, a figure similar to wolf predation on moose on Isle Royale (Peterson 1977). Peterson suggested that when carcass utilization was unknown, a measure of food availability rather than food consumption was obtained. Based on carcasses only, the meat available to wolves on Isle Royale varied from 6.2 to 10.0 kg per wolf per day during 1971-1973, and 4.4 to 5.0 kg during 1974 on Isle Royale. In view of the presence of both avian and mammalian scavengers in Wood Buffalo National Park such observations may also be applicable to the wolf/bison ecosystem. However, because our data described virtually complete utilization of kills by the Hornaday River pack soon after they were made, we considered food availability in our case to approach or equal consumption.

The Hornaday River pack scavenged on five bison carcasses in 1978-1979, two in 1979-1980, and none in 1980-1981. The cause of death of four of these was unknown; the other was killed by an adjacent pack (Salt River), which was displaced from the kill by the Hornaday River pack in late February 1980. In all cases, 75% to 100% of each carcass was already consumed when the pack visited them, and thus meat left over contributed little to the overall amount of food required by the pack during these periods of observation.

Prey biomass consumption appeared to be higher in 1978-1979 than in 1979-1980 or 1980-1981 (6.2 versus 3.4 and 4.8 kg per wolf per day). The difference could be attributed to the severe winter of 1978-1979. Although the rate at which bison were killed was higher in 1979-1980 than in the other winters, selection was primarily for calves, which reduced the per capita biomass consumed. Unlike deer killed by wolves in Minnesota (Mech 1977) and elk in Manitoba (Carbyn 1980), there was no evidence of a significant increase in predation rate or biomass consumption from early to late winter in any of the winters from 1978 to 1981.

Predation rate by the Hornaday River pack was similar to those by wolves in the Slave River Lowlands. Van Camp (1987) reported that over a six-week period in early winter, a pack of 12-14 wolves consumed a minimum of six bison, or approximately one per week, although he felt that the overall winter predation rate for each pack (average size 11 wolves) was closer to one adult every nine days, as well as one calf every 15 days.

Food consumption by wolves in winter in Wood Buffalo National Park was somewhat higher than that published for wolves preying on deer. In Ontario, Pimlott et al. (1969) and Kolenosky (1972) estimated a daily rate of consumption of 3.81 and 2.93 kg per wolf, and Mech and Frenzel (1971) calculated a rate of

consumption in northeastern Minnesota of 2.74 kg per wolf per day. However, on Isle Royale, wolves preying on moose consumed an average of 5.6 kg per wolf per day over three winters of observation (Mech 1966). In Riding Mountain National Park, wolves and scavengers (to an unknown degree) consumed 6.7 kg of prey per wolf per day under unusual severe winter conditions and high elk densities (Carbyn 1981). Differences in food consumption between the various study areas mentioned may be partially explained by size differences and energy requirements of the wolves under study. Based on the weights of our captured animals, wolves in the Hornaday River pack weighed an average of 43 kg for females and 50 kg for males, and were substantially larger than those found in eastern North America.

Information supporting a direct relationship between pack size and prey consumption was not obtained and conclusions await further study. Predation rates were highest in 1979-1980 when the Hornaday River pack was largest, but prey biomass consumed by each pack member was lowest that winter, suggesting that abundance and vulnerability of bison may have been dominant factors, which determined bison consumption by wolves, rather than pack size. Prey biomass consumption by the Hornaday River pack was similar in the winters of 1979-1980 and 1980-1981 when pack size differed the most.

ii) Prey selection

Ages of 131 bison killed by wolves in winter from 1971 to 1981 (Figure 45), compared with the estimated winter age structure of the population (Table 44), showed that calves were selected for disproportionately when compared to their presence in the population (24% versus 11%), while bison between two and five years were relatively immune to wolf predation. Bison aged five years and older were killed at a rate slightly higher than their presence in the population, but this difference was not significant ($p > 0.05$).

From 1978 to 1981, winter kills recorded for the Hornaday River pack consisted of 12 adult male bison, 16 adult females, three yearlings, and 17 calves. Comparison of ages of these wolf-killed bison to the estimated age structure of the population (Table 44 and 45) revealed a similar pattern of selection to that of 1971 to 1981 from "kills" reported by wardens. The latter may be somewhat biased as, without radio-tracking, some of the "kills" may have been scavenged rather than killed by wolves. Predation on calves and old bison (11+ years) from radio-tracking data was particularly high (Figure 45).

The kill ratios of adult male to female bison occurred in proportion to their estimated abundance in the population (104 bulls:108 cows, Novakowski 1958; 95 bulls:115 cows, Fuller 1951; 2,624 bulls:2,687 cows in this study). Kill ratios for 1971-1981 by the Hornaday River pack was 39:41, for the winter 1978-1981 was 12:16, and for the non-collared wolves from 1978-1981 was 15:19.

Prey selection by the Hornaday River pack for calves versus adult bison was determined from available prey based on early winter aerial surveys, and number of calves and adults killed during each winter from 1978-1979 to 1980-1981 (Table 45). Calves killed were disproportionately higher than available in all years, except

for in 1978-1979. It is probable that herds with calves were less available in the study area that year. Prey selection varied from entirely adult bison in 1978-1979 to 50% and 43% calves in 1979-1980 and 1980-1981, respectively (Table 45). Conversely, with the exception of 1978-1979 by the Hornaday River pack, wolves in all years killed adult bison less than expected from their observed presence, although the differences between availability and numbers killed were less for non-collared wolves than for the Hornaday River pack in the winters 1979-1980, 1980-1981, as well as the 1978-1981 aggregate.

The mean proportion of marrow fat in femurs collected from 72 wolf-killed bison in the Park from winters 1977-1978 to 1980-1981 was 73% and ranged from 7% to 99% (Figure 46). Mean marrow-fat values for adult males killed were the lowest (67%, n = 25), followed by adult females (76%, n = 32), and calves (81%,

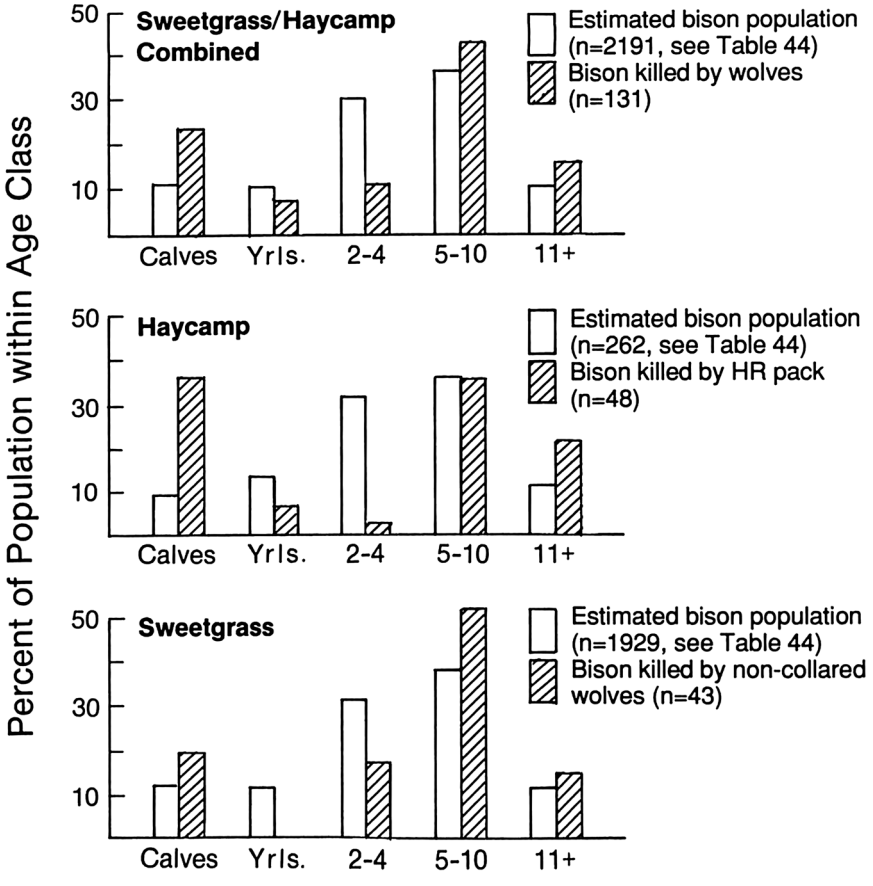


Figure 45. Age distribution of bison available to, and killed by wolves in Wood Buffalo National Park, 1971 to 1981. HR=Hornaday River pack.

Table 44. Age structure of bison available to, and killed by wolves in early, mid, and late winter, 1971 to 1981.

Age class (years)	Number of bison: Sweetgrass Total[1]	Sweetgrass Adjusted total[2]	Sweetgrass Percent	Sweetgrass Percent killed by wolves (NCW)	Hay Camp Total[3]	Hay Camp Adjusted total[2]	Hay Camp Percent	Hay Camp Percent killed by wolves (HR pack)	Combined Total	Combined Adjusted total	Combined Percent	Combined Percent killed by wolves (total)
Calves	134	218	11.3	18.6	43	23	8.8	35.4	177	241	11.0	23.7
Yearlings	208	198	10.3	0.0	32	35	13.4	6.3	240	233	10.6	7.6
2-4	616	586	30.4	16.3	75	82	31.3	2.1	691	668	30.5	10.7
5-10	966	719	37.3	51.2	112	94	35.8	35.4	1078	813	37.1	42.7
11+	5	208	10.8	14.0	0	28	10.8	20.8	5	236	10.8	15.3
Total	1929	1929	100.1	100.1	262	262	100.1	100.0	2191	2191	100.0	100.0

[1] Novakowski and Choquette (1964).

[2] Based on 1978-1980 mean calf proportion (Hay Camp 8.8%, Sweetgrass 11.3%) from early winter aerial surveys, and adjusted proportion of aged bison (10.8%) in 1971 field slaughter (Currier 1971).

[3] Novakowski and Choquette (1963).

NCW = non-collared wolves; kills by these occurred primarily in the Peace-Athabasca Delta.

Table 45. Estimated age structure (adults[1]/calves of the bison population in early winter[2]), and bison killed by wolves in winter in Wood Buffalo National Park; 1978-1979, 1979-1980, and 1980-1981.

		NUMBER OF BISON							
		Hornaday River Pack[2]				Non-collared wolves[4]			
		Number available	Percent	Number killed	Percent	Number available	Percent	Number killed	Percent
1978-79[3]	Calves	5	2.9	0	0.0	166	11.5	3	27.3
	Adults	174	97.1	12	100.0	1272	88.5	8	72.7
Totals		179	100.0	12	100.0	1438	100.0	11	100.0
1979-80[3]	Calves	69	7.8	11	50.0	200	9.2	2	20.0
	Adults	814	92.2	11	50.0	1966	90.8	8	80.0
Totals		883	100.0	22	100.0	2166	100.0	10	100.0
1980-81[3]	Calves	96	11.0	6	42.9	425	12.5	3	14.3
	Adults	774	89.0	8	57.1	2969	87.5	18	85.7
Totals		870	100.0	14	100.0	3394	100.0	21	100.0
All years	Calves	170	8.8	17	35.4	791	11.3	8	19.0
	Adults	1762	91.2	31	64.6	6207	88.7	34	81.0
Totals		1932	100.0	48	100.0	6998	100.0	42	100.0

[1] All bison older than yearlings.

[2] All are early winter counts, except 1978-1979, which is midwinter (radio-tracking commenced 9 February 1979).

[3] Hornaday River pack home range: 1978-1979 - Hay Camp and Darough Creek Prairies; 1979-1980 - Raup Lake, Murdock Creek Meadows; Hay Camp and Darough Creek Prairies; 1980-1981 - Raup Lake Meadows; Hay Camp and Darough Creek Prairies.

[4] All other primary bison ranges.

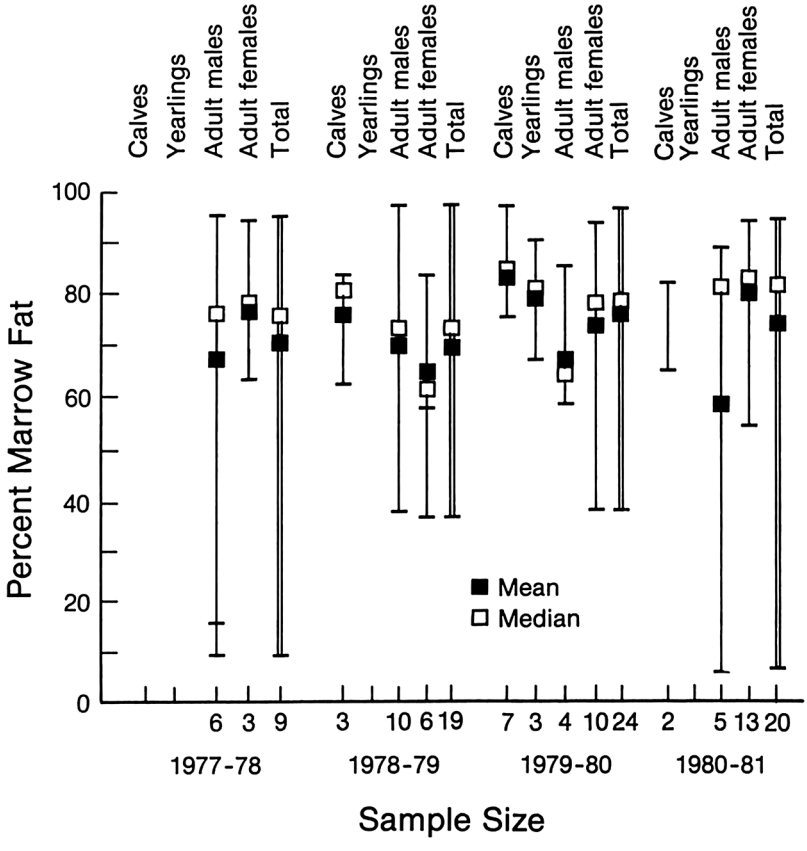


Figure 46. Percent marrow-fat distribution of 72 wolf-killed bison, segregated by age in Wood Buffalo National Park, 1977 to 1981 combined.

n = 12). Marrow-fat values for adult males were significantly less ($p < 0.05$) than those for other age/sex groups. Older age classes of both male and female bison also had lower marrow fat than younger bison (see Figure 47), and values for old males were lower than those for old females. Marrow-fat values for all bison combined were lowest in 1978-1979 (Figure 47), although those for adult males were lowest in 1979-1980. Mean marrow-fat values for bison calves were highest in 1979-1980, and did not support our earlier suggestion that calf condition and viability may have been reduced in years following a severe winter.

Marrow-fat values for wolf-killed bison decreased from early to late winter (Figure 48), but these changes were not statistically significant (Kingsley 1982). A decrease was most noticeable for adult males, and may have reflected an expected decline in condition for the bison population at large as winter progressed. If sex has an influence on condition and if both sexes have an equal chance of infections by the diseases, then sex differential conditional factors appear to indicate that

disease is less important in the condition of the animals than are other factors. Wolf predation pressures on calves was relatively constant throughout the winter (Table 42).

When the condition of wolf-killed male bison, and the apparent ease with which they were killed in one year (1978-1979) are considered together, it is likely that the nutritional plane of all male bison in the population during early and midwinter was lower than that of females and young bison. Although this is not entirely in agreement with observations of bison in the Mackenzie Bison Sanctuary (C. Gates, pers. comm.), adult bull moose and elk lose weight during the rut (Flook 1971, McGillis 1972, Franzmann et al. 1978); they are unable to recover this substantial loss before the onset of winter, and thus may show the effects of a negative energy balance before females do. Mature male caribou apparently also

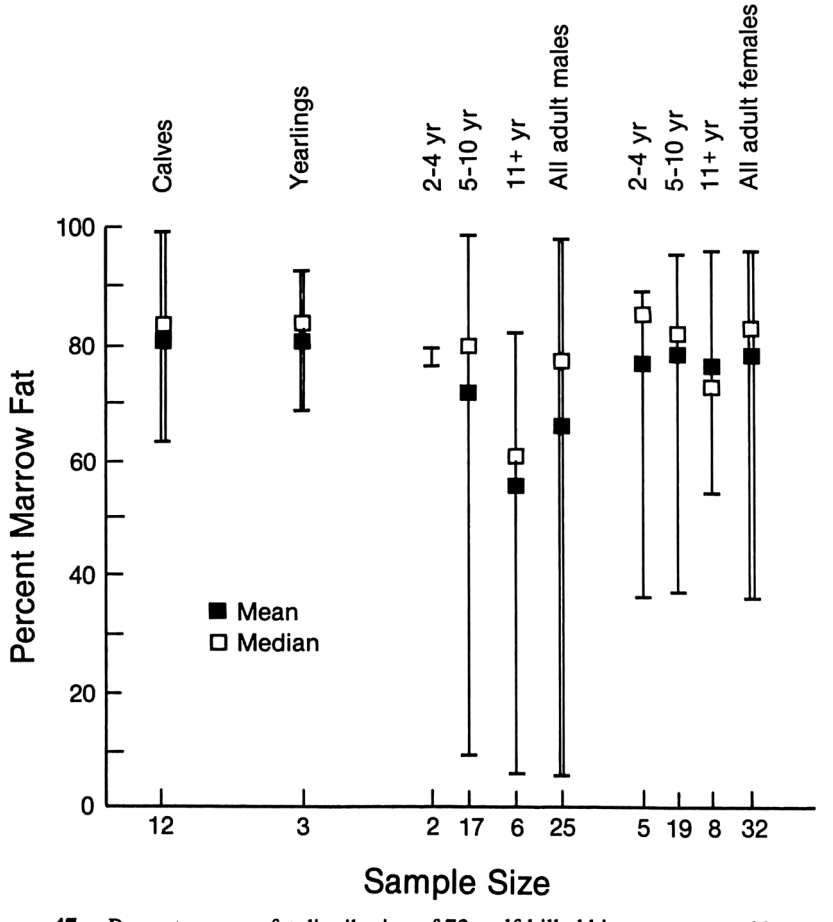


Figure 47. Percent marrow-fat distribution of 72 wolf-killed bison, segregated by age in Wood Buffalo National Park, 1978 to 1981.

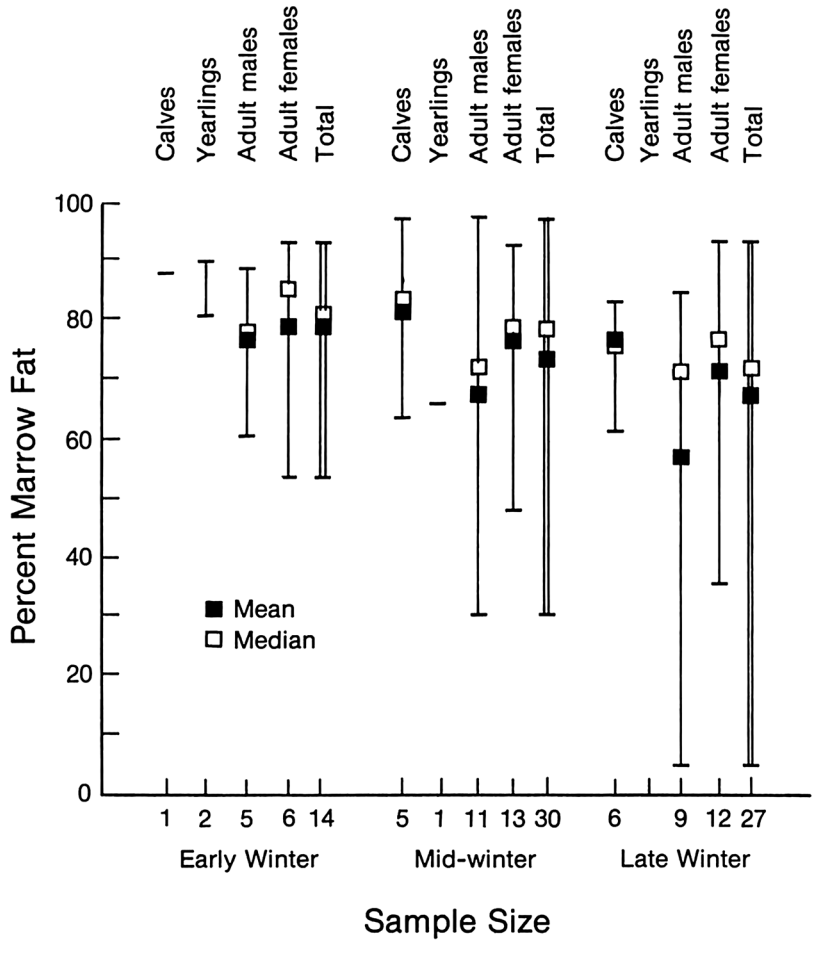


Figure 48. Percent marrow-fat as determined from 72 wolf-killed bison in Wood Buffalo National Park for early, mid, and late winter periods, 1977 to 1981.

enter the winter in poorer condition than females (Dauphine 1976). Adult male bison eat sparingly, yet are extremely active during the rut (Lott 1978), and likely enter the winter with lower fat reserves than females and younger bison. The energy losses are possibly replenished more quickly during years with mild to moderate winter conditions.

iii) Wolf hunting strategy in winter

Sixty-five wolf-prey encounters were observed from aircraft in Wood Buffalo National Park during the four winters 1977-1978 to 1980-1981. Sixty-three of these were of wolves and bison, and two of wolves and moose. In 29 of the wolf-bison

encounters, the wolves merely watched their prey, and in another 18 the wolves deliberately approached their prey, but did not attack (Table 46).

Wolves concentrated primarily on herds (56 of 63 observations). Differences in prey targets between winters 1978-1979 and 1980-1981 were not proportional to the available prey types (Table 47). Hunting success of wolves preying on bison was determined in four ways:

(1) as the number of successful attacks versus number of approaches and attacks observed, e.g., "testing" prey (Mech 1966, Peterson 1977);

(2) as the number of successful versus unsuccessful chases, based on aerial observations of wolves and interpretation of tracks (Kolenosky 1972);

(3) as the number of successful versus total encounters for various time periods that wolves were with prey; and

(4) as the known number of prey killed versus the total number of encounters observed.

The wolves attacked on 13 occasions, and were successful in killing a target animal on three occasions. In the first instance, the wolves approached or attacked bison on 31 occasions (Table 46) and killed an animal on three, or 9%, of these testing sequences. Secondly, wolves were successful on 33% of 86 chases observed from the air, or reconstructed from track evidence during the winters 1978-1979 to 1980-1981 (Table 48). There was no noticeable difference between 1979-1980 and 1980-1981, although in the small number of observed chases in 1978-1979, there was a high overall success rate for that year.

Table 46. Summary of aerial observations of wolf-bison encounters[1], winters 1977-1978 to 1980-1981, Wood Buffalo National Park.

Year	Watching Prey	Approach Prey And Retreat	Prey Attacked[2]	Prey Killed	Total
1977-78	2	1	-	-	3
1978-79	5	1	-	-	6
1979-80	12	9	7	2	30
1980-81	10	7	6	1	24
TOTAL	29	18	13	3	63

[1] Excludes multiple chase sequences observed on the same day.

[2] Charged and chased.

Table 47. Predation in relation to available prey[1] for wolves north of the Peace River (Area I), winters 1978-1979 to 1980-1981.

	1978-79			1979-80			1980-81			Total 1978-81		
	Available prey types	Encounters	Kills found	Available prey types	Encounters	Kills found	Available prey types	Ecounters	Kills found	Available prey types	Encounters	Kills found
Total observations	56	6	9	52	30	16	71	24	13	180	60	38
Bull-groups and solitary animals[2]	82.2	50.0	77.8	73.0	6.7	12.5	81.7	8.3	15.4	78.9	11.6	28.9
Herds	17.8	50.0	22.2	27.0	92.3	87.5	18.3	91.7	81.6	21.1	88.4	71.1

[1] Based on observation from midwinter annual total counts of Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows.

[2] May include adult cows.

Table 48. Hunting success of wolves based on proportion of successful chases, as determined from aerial observations and track evidence, winters 1978-1979 to 1980-1981, Wood Buffalo National Park.

	Number of Bison Chases			Successful Chases					
				Observed		Tracks		Total	
	Observed	Tracks	Total	Number	Percent	Number	Percent	Number	Percent
1978-79	1	7	8	0	0.0	7	100.0	7	87.5
1979-80	30	9	39	2	6.7	9	100.0	11	28.2
1980-81	15	24	39	1	6.7	9	37.5	10	25.6
Total	46	40	86	3	6.5	25	62.5	28	32.5

When the success rate was based on the wolves' prior presence with prey (Table 49), wolves succeeded in killing a bison out of a herd on 73% of the times they were with herds less than one day, and 100% when they were with herds for more than three days. On five occasions, the wolves stayed with potential prey more than one day, e.g., they were seen on two consecutive days with the same herd, and they left without killing a bison. Four of these instances, however, occurred less than three days after the wolves had made a previous kill; the other resulted in a kill from the same herd two days later. On one other occasion, the wolves spent less than one day with a herd before leaving unsuccessfully the next day, then returned to the same herd a day later and killed a bison after three days with the herd.

Table 49. Hunting success of wolves in relation to previous encounters with potential prey, winters 1978-1979 to 1980-1981, Wood Buffalo National Park.

	Number of days observed with same herds[1]					
Killing success	**<1**	**1-2**	**2-3**	**3-4**	**4+**	**Total**
Unsuccessful	3	3	2	0	0	8
Successful	8	6	2	4	2	22
Total	11	9	4	4	2	30
Success rate (%)	73	67	50	100	100	73

	Number of days observed with same bull-groups, solitary bison, moose[1]					
	<1	**1-2**	**2-3**	**3-4**	**4+**	**Total**
Unsuccessful	5	0	-	-	-	5
Successful[2]	10	1	-	-	-	11
Total	15	1	-	-	-	16
Success rate (%)	67	100	-	-	-	69

[1] Includes all forms of encounters with prey (Table 47) followed by abandonment (unsuccessful) or killing of prey (successful).

[2] Includes one adult male bison and one adult female moose killed by members of the Salt River pack in 1979-1980 and 1980-1981.

When the two latter instances were included as successful encounters, the overall success rate for wolves preying on herds increased from 73% to 79%. The wolves' overall success rate with bull groups, solitary bison, and moose (Table 49) was less (69%) than that for herds, and the majority of these kills occurred within the first 24 hours of contact with the prey. The relative success rate for the Hornaday River pack was higher in 1978-1979, when the number of encounters per pack observation was lowest, and the number of kills per encounter was highest (Table 50). This pattern of success for the Hornaday pack that year appeared to be related to predation on bull groups and solitary bison. In every winter, success was highest for these prey types (Table 51), which may be an indication that the wolves will key in on vulnerable prey when they have a way of "knowing" when the prey is vulnerable.

An analysis of the Hornaday River pack's association with potential prey for which the outcome was observed indicated that the pack was generally more successful in securing a kill if the kill was preceded by some form of previous encounter (Table 52). Of the 52 encounters observed, 18 (35%) resulted in kills within 24 hours, whereas 6% of non-encounters, i.e., where no previous associations were recorded, resulted in kills within a day.

Similarly, a review of repeated attacks on bison herds by the Hornaday River pack showed that ten of the 12 repeated attacks on herds were successful (Table 53). Exceptions occurred on 14-15 February 1980 and 22-23 March 1980, when the wolves had already killed a yearling bison from the same herd a day earlier (13 February), and when the pack killed an adult cow out of an adjacent herd the next

Table 50. Relative hunting success of the Hornaday River pack, expressed as number of kills found per encounter; winters 1978-1979 to 1980-1981, Wood Buffalo National Park.

Year	Number of observations[1]	Number of wolf-prey encounters[2]	No. of kills found	Number of encounters per observation	Number of kills per encounter
1978-79	47	4	10	0.085	2.50
1979-80	92	32	19	0.348	0.59
1980-81	71	24	13	0.312	0.54
Total	216	60	42	0.277	0.70

[1] November to April, inclusive.

[2] Excludes multiple chase sequences observed on the same day.

Table 51. Relative hunting success of the Hornaday River pack, expressed as number of kills found per encounter[1] for various prey types, winters 1978-1979 to 1980-1981, Wood Buffalo National Park.

	1978-79			1979-80			1980-81			Total 1978-81		
Prey type	**# of encounters**	**# of kills**	**# kills/ encounter**	**# of encounters**	**# of kills**	**# kills/ encounter**	**# of encounters**	**# of kills**	**# kills/ encounter**	**# of encounters**	**# of kills**	**# kills/ encounter**
Herds	2	2	1.0	28	14	0.5	22	11	0.5	52	27	0.5
Bull-groups and solitary bison[2]	2	7	3.5	2	2	1.0	2	2	1.0	6	11	1.8
Moose				2	1	0.5				2	1	0.5

[1] Excludes multiple chase sequences observed on the same day.

[2] May include adult cows.

Table 52. Hunting success of the Hornaday River pack, based on the pack's prior association with potential prey; winters 1978-1979 to 1980-1981, Wood Buffalo National Park.

Type of association	1978-79		1979-80		1980-81		Total 1978-81	
	Observations	Kills[3]	Observations	Kills[3]	Observations	Kills[3]	Observations	Kills[3]
Non-encounters	38	5	47	0	55	3	140	8
Encounters[1]	2	0	30	12	20	6	52	18
Unknown[2]	5	5	15	6	8	4	28	15
Total	45	10	92	18	83	13	220	41

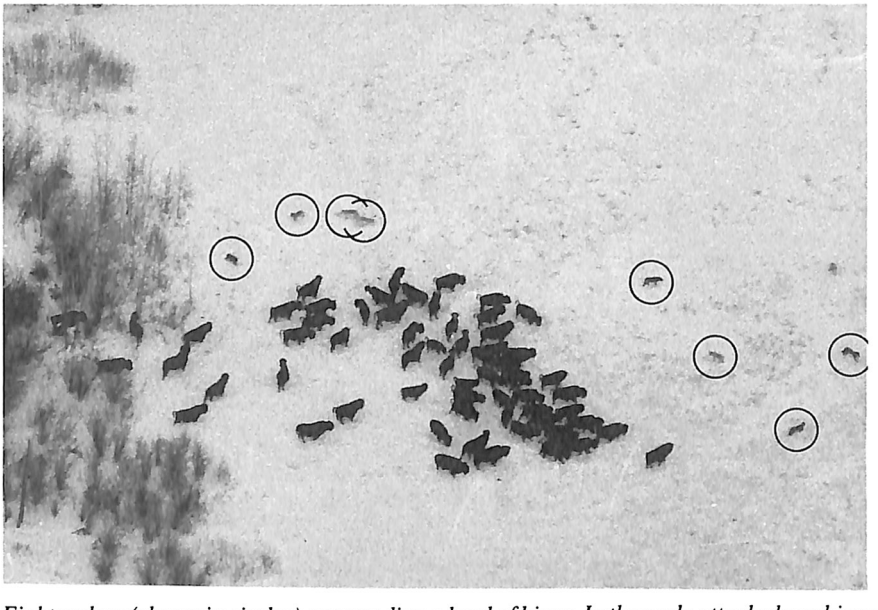
[1] Excludes multiple chase sequences observed on the same day.

[2] Wolves not sighted.

[3] Kills made within 24 hours of observation on previous day.

Wolves kill all age classes and both sexes of bison within Wood Buffalo National Park. A full grown bull weighs around 1,000 kg and is a formidable adversary, which requires co-operative hunting strategy to pull down.

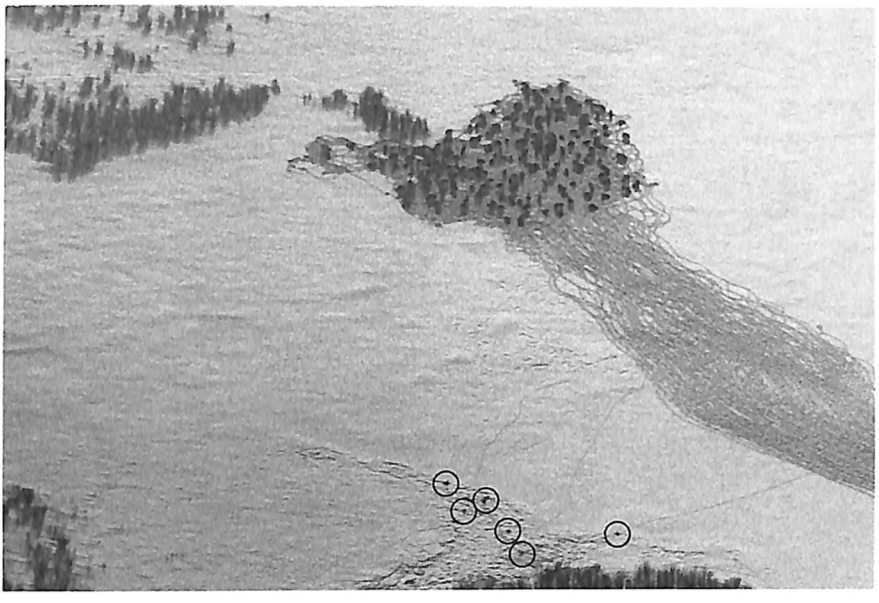
Aerial view of a bison herd foraging in a scattered formation on sedges near the Peace-Athabasca Delta of Wood Buffalo National Park. Bison crater the snow, using their heads, in order to get to the sedge cover.



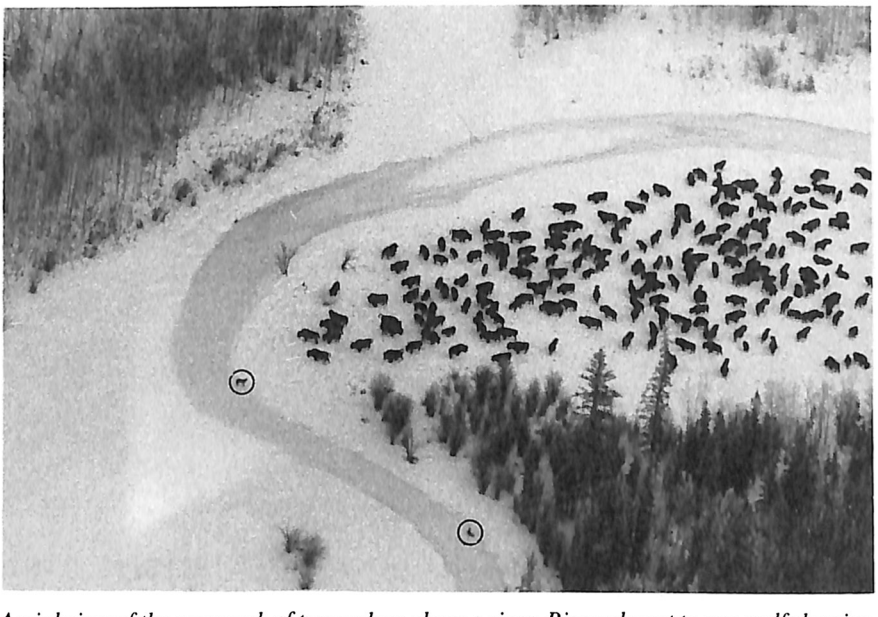
Eight wolves (shown in circles) surrounding a herd of bison. In the early attack phase bison respond by becoming alert, and bunching together. If attack persists, the herd will stampede, allowing wolves to pursue, isolate an individual, and attempt to pull it down.

A cow has been isolated from the herd and is being pursued by the pack. Note attack by the wolf at the soft portion on the hind quarters.

The pack is closing in on the victim. After tearing at the hind quarters, single or pairs of wolves will attempt to grab the nose and pull the prey down.



Not all chases are successful. Beaded tracks in the snow indicate the flight path of the herd, having run in a tight formation and stopped to rest; exhausted wolves rest nearby. Such chases can go on for several kilometres. In one case a pack had killed a bison within a 4.3 km chase, and then the herd continued to move for another 86 km before resting.



Aerial view of the approach of two wolves along a river. Bison closest to one wolf showing early signs of alarm, by facing the wolf.

Table 53. Summary of repeated attacks[1] on bison herds by the Hornaday River pack, winters 1979-1980 and 1980-1981, Wood Buffalo National Park.

Herd number	Herd size	Date	Evidence of chase[2]	Chase distance (km)	After-kill flight distance (km)	Number of days with herd[3]	Number of previous kills from same herd
1	60	15/12/79	t	2.55	7.88	?	?
	60	17/12/79	t	4.94	7.11	2-3[4]	1
2	40	21/12/79	o	0.90	-	1	?
	40	22/12/79	t	3.99	8.01	1-2	?
3	65	13/02/80	t	0.20	3.15	1	?
	65	14/02/80	o	0.65	-	1-2	?
	65	15/02/80	o	0.92	-	2-3	?
4	90	20/02/80	t	0.10	6.48	1-2	?
	199	23/02/80	t	0.15	27.35	1	1
	120	02/03/80	o	0.07	13.18	?	2
5	23	10/03/80	t	0.10	11.51	4-5	?
	23	12/03/80	o	0.42	-	1-2	1
	43	14/03/80	t	0.30	9.53	3-4	1
	23	08/03/80	ot	16.16	-	2-3	?
	23	09/03/80	t	8.00	-	3-4	?
6	39	22/03/80	t	2.00	-	1	?
	47	23/03/80	t	2.50	-	1-2	?
7	90	08/02/81	o	0.18	-	1	?
	90	09/02/81	ot	0.52	-	1-2	?
	90	10/02/81	t	6.17	-	2-3	?
	90	14/02/81	t	0.20	-	1-2	?
	90	16/02/81	t	0.05	19.45	3-4	?
	90	06/03/81	t	1.00	-	1	1
	90	07/03/81	t	7.20	-	1-2	1
	90	09/03/81	t	4.30	81.45	3-4	1
8	300	25/02/81	t	3.20	0.80	1	?
	300	27/02/81	ot	1.62	-	1	1
	300	28/02/81	t	0.80	-	1-2	1

Table 53. Continued.

Herd number	Herd size	Date	Evidence of chase[2]	Chase distance (km)	After-kill flight distance (km)	Number of days with herd[3]	Number of previous kills from same herd
	230	28/02/81	t	6.10	-	1-2	1
	230	01/03/81	t	2.53	-	2-3	1
	230	02/03/81	t	0.76	-	3-4	1
	75	02/03/81	t	0.70	47.50	3-4	1
	22	18/03/81	o	6.25	-	?	2
	22	19/03/81	t	1.30	18.07	1-2[4]	2
9	25	23/03/81	t	3.40	-	1	?
	25	24/03/81	o	2.20	1.35	1-2	?
10	31	09/04/81	o	0.05	-	1	?
	26	14/04/81	t	0.80	?	3-4	?

[1] Charges and chases.

[2] Interpretation of chase based on: o = actual observations, t = track evidence, ot = observation and track evidence.

[3] Includes all forms of encounters with bison herds (Table 46) on consecutive days.

[4] Figures for the same herd are minimum values.

day (24 March). In three cases, a minimum of two known bison (all calves) were killed out of the same herd over the course of the winter.

It was possible to document the Hornaday River pack's behaviour in relation to the number of days since its last known kill for 31, 73, and 71 observations in 1978-1979, 1979-1980 and 1980-1981. Although in each winter the mean number of days since its last known kill was predictably greater for encounters than for non-encounters, there was no apparent pattern of increasing "active" interest in prey, i.e., approaching, attacking or killing prey, with increased duration since the last kill (Figure 49). Kills resulting from encounters became more certain as time from last kill increased. Kill rates were greatest in 1980-1981 and least in 1979-1980. In all instances except one, medians were less than mean values (Figure 49). In this case, most kills in 1978-1979 occurred in the higher range of days since the last known kill.

Little is known about hunting success of wolves, or how many times a pack has to attack before it becomes successful. Mech (1966) and Peterson (1977) used the term "testing" where moose were approached or attacked, and reported that

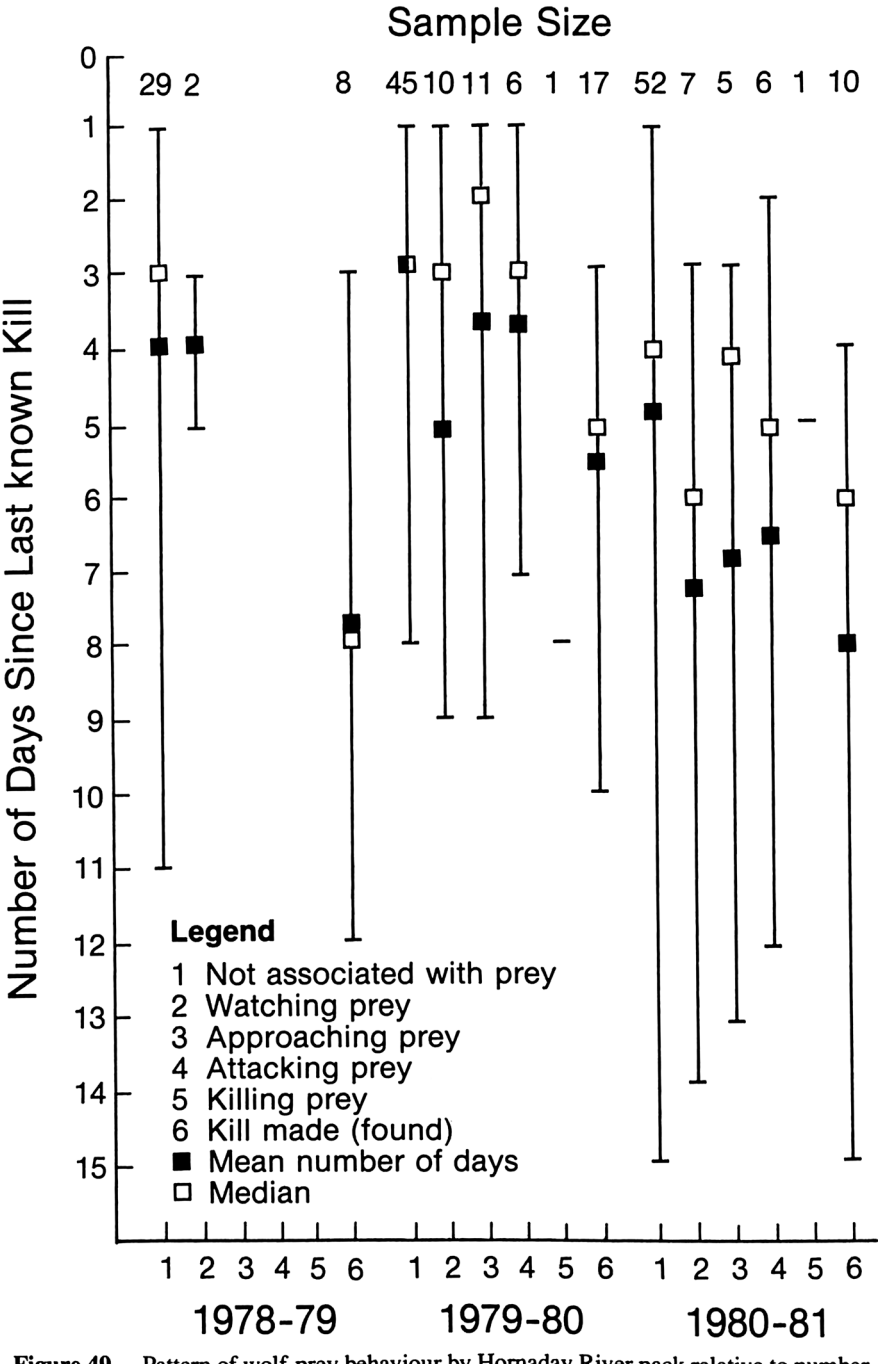

Sample Size
29 2 8 45 10 11 6 1 17 52 7 5 6 1 10
Number of Days Since Last known Kill
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Legend
1 Not associated with prey
2 Watching prey
3 Approaching prey
4 Attacking prey
5 Killing prey
6 Kill made (found)
■ Mean number of days
□ Median
1 2 3 4 5 6 1 2 3 4 5 6 1 2 3 4 5 6
1978-79
1979-80
1980-81

Figure 49. Pattern of wolf-prey behaviour by Hornaday River pack relative to number of days since last known kill, 1978 to 1981.

wolves killed between 3 and 8% of the prey they tested. Using these criteria, bison hunting success of 9% (Table 46) was similar to that proposed for moose by Mech (1966). This definition however, implied that the wolves only used approaches or attacks to test prey. Wolves undoubtedly recognized vulnerable traits in prey that were not obvious to the aerial observers, and thus the observed hunting success may have been exaggerated. In Ontario, Kolenosky (1972) reported that wolves succeeded on 25% of their hunts on deer in one winter, and 63% during another, but speculated that these rates may have been inflated because they were based entirely on track evidence often originating from a kill site. In our study, we used a combination of aerial observations and interpretation of tracks to document an overall success rate of 33% over the three winters, and noted that hunting success based on track evidence only, was much higher than that based on actual observations of chases.

The success rates quoted in previous studies applied to kills on solitary prey or relatively small groups, whereas wolves hunting bison preyed primarily on herds, where more individuals may have been potentially vulnerable. The hunting success rate of wolves attacking herds was somewhat higher than for wolves hunting solitary prey. Comparable information comes from another pack hunting species, the African hunting dog (*Lycaon pictus*), which preys primarily on herds. Hunting dogs apparently have a hunting success rate from about 34% (Van Lawick-Goodall 1971) to 85% (Estes and Goddard 1967). Hunting success for any species, however depends ultimately on the vulnerability of the prey (i.e., age, condition), the efficiency of the hunting unit, as well as environmental conditions leading up to, and at the time of the encounter.

Our data suggest that success rates increased with increased time spent with prey. A similar situation occurred for wolf predation on moose on Isle Royale. If packs there did not kill quickly, they often left wounded moose and began to search for other prey (Peterson 1977). Wolves in Wood Buffalo National Park stayed with herds, or in areas with herds, for up to six days before making a kill. Their presence with herds is likely a result of differences in prey distribution patterns. It is easier to retain contact with bison herds than more randomly dispersed solitary prey such as moose and deer.

Instances of wolves attacking the same herd on repeated occasions, often more than once successfully, can also be explained in terms of wolf energetics and searching effort. Herds which were attacked more than once may have been easier targets than those which had first to be located, because wolves knew where they were from tracks leading away from the previous pursuit or kill site. It is possible that the wolves purposely followed these herds in anticipation of isolating debilitated individuals, either from recognition or prior wounding. Fuller (1966) reported instances of wolves having previously wounded bison before eventually killing the animals at a later date. Alternatively, it could be advantageous for wolves to leave herds that are in a state of alert, and prey on animals not agitated by the presence of wolves, and then return to the original herds at a later time.

iv) Killing Strategy

An adult bison is a formidable target for a pack of wolves to kill. Detailed descriptions of how wolves kill bison is scant. Garretson (1938) described one graphic and sensationalized incident related to him of wolves attacking and wounding a bull. During his studies of bison in Wood Buffalo National Park in the 1950s, Fuller (1960, 1966) described several wolf attacks and examined a number of bison wounded or killed by wolves. Wolves appeared to always single-out one animal in a herd, which might be the subject of repeated attacks if the first attack was unsuccessful.

Once wolves were able to isolate an individual from a herd, or surround a solitary animal, they generally attacked the rear of the bison in an attempt to wound and incapacitate the hind leg muscles (Table 54). Depending on the reaction of the bison, the wolves would continue to tear at the hindquarters as the bison circled to ward off the attack with its head, or would hold on to the bison's hind legs as it attempted to escape. A calf was held similarly while other members of the pack tried to knock it off its feet. Local residents from Fort Chipewyan and from Fort Smith have often reported incidences of severe mauling of bison that have escaped. Wounded calves were repeatedly seen in May and June of 1990 and 1991. One wounded calf seen in October 1990 was attended by its dam for at least 6 days. The

Table 54. Summary of wounding in bison killed by wolves[1] in Wood Buffalo National Park, winters 1978-1979 to 1980-1981.

Date	Group size	Number of wolves	Estimated age of prey[2] (year)	Sex	Primary areas of wounding
19/01/79	3-5	14	6	Bull	Rump, anus, nose (?)
26/01/79	35	7	10	Cow	Rump, shoulder
30/03/79	70	6	1	Cow	Hind legs, flanks
21/04/79	?	6	Adult	Cow	Anus, shoulder
10/01/80	?	6	Adult	Cow	Flanks, abdomen
18/02/80	1	7	7	Bull	Flanks, rump
02/03/80	120	10	1	Bull	Rump, shoulder
16/02/81	98	8	8	Cow	Rump, flanks
24/03/81	25	8	12	Cow	Flanks, Anal area

[1] Determined from aerial observations or examination of freshly killed bison.

[2] Determined by cross section of incisor and examination of horn annuli.

calf was suffering from, what appeared to be, a severe case of blood poisoning. A commensal bacteria, *Pasturella multocida* is known to be in the mouths of carnivores, which when transferred to a wound will cause infections.

In three instances during our studies in winter, we observed wolves making contact with bison, where an individual did not escape, and was observed being killed. On two other occasions, contact was suspected, but not confirmed, and the bison managed to rejoin the herd. An example of a bison being separated from a herd and unable to catch up with it again occurred on 24 March 1981, when we observed eight wolves chasing a herd of 25 bison in the northwest corner of the Darough Creek meadows. The sequence was as follows:

> "At 0940, the Hornaday River pack was running approximately 1 km behind the main portion of a herd of 25 bison. The wolves were running in single file over a distance of 500 m, led by one wolf, which was at least 100 m ahead of the others. Two groups of bison, one of seven, and one of two animals, had stopped running and were standing in the line of the chase. At 0942, the lead wolf reached the second group of bison, after having run past the first group of seven bulls. The two bison put their heads down and charged the wolf as it ran past them, and they chased it for 10 m as the wolf continued after the group of 16 that was running southeast. Two other wolves ran by the two bison (both cows) at 0943, but the remainder of the pack began to harass these two as they reached them by 0944. As soon as the first three wolves realized the rest of the pack was attacking the two bison, they ran back and joined the attack. By 0945, all the wolves were circling, lunging, and snapping at the two cows, but one of these managed to run from the wolves, whereupon the pack concentrated its attack on the remaining bison. Between 0945 and 0955, the wolves were pressing all around the cow, trying to get at it from the rear, biting the rump and anal area. The cow tried to ward off the attack with its head, but the wolves continued to circle to the rear with the result that the cow was continually turning in circles. In the meantime, the cow tried to run after the herd, which at this point was at least 1 km away, and still moving into the open meadows. Trail conditions allowing, the wolves would grab and tear the cow's flanks, and where the trail was narrow, they would follow in file until the trail widened, and several wolves would grab at the cows hind end. During much of the pursuit, one of the wolves ran in front of the bison, possibly to distract it or to attempt to grab the muzzle. At 0955, the bison was visibly tiring as it struggled through the snow with several wolves hanging on its hindquarters. The harassment and wounding had taken place over 750 m from the first confrontation to where the cow had dragged itself into the trees to face the wolves. By 1000, both wolves and bison were in the trees. The cow had stopped running, but the wolves continued the attack, coming in from behind and wounding the cow. Two light-coloured wolves were covered with blood; several wolves were resting as the others continued to press. At 1005, the bison was standing in the trees, its hindquarters shaking. As it fell over once, the wolves closed in on it immediately and began to tear at its' abdomen. The cow managed to get up and dragged itself 10 m with several wolves holding on to its hindquarters. At 1007, the bison was still on its feet, standing and facing the wolves with its tail up. Some of the wolves were resting nearby, and the bison lunged at several standing close; the wolves stepped back. At 1015, the bison was down; although its head was still up, the wolves were tearing at its abdomen. By 1030, the wolves were feeding, the bison's head rose occasionally, but it was close

to death. The herd of 16 had stopped 800 m to the southeast at the edge of the open meadow and some were beginning to graze."

Examination of the carcass the next day showed that this was a mature cow. Damage was almost entirely restricted to the hindquarters. The body was intact, except for holes in the flanks and anal area; all the internal organs had been removed from the body cavity and consumed. Evidence of pregnancy included a portion of a fetal hoof at the kill site.

The following account describes the killing of an adult male bison where wolves again concentrated on the posterior region of the bison, and were observed hanging onto its tail during the attack.

"On 18 February 1980, we spotted a pack of seven wolves resting on the bank of the Salt River. We returned to Fort Smith for a helicopter to capture members of the pack. At 1310, the pack was located 1.2 km east of its original position in the process of attacking a solitary bull. From the trampled areas, it appeared the bull had probably been under attack since 1300, and had fought off the wolves at four locations prior to our arrival. Between 1310 and 1330, the wolves attempted to get at the rear of the bull, while it kept spinning around to face and fend off the wolves with its head. The bull broke into a run several times with some of the wolves hanging on to its flanks, rump, and tail. It ran into some willows on three occasions and was unable to partially shake the intensive attack of the wolves. Attacks were almost continuous, with several of the wolves darting in from the rear and grabbing the bison's hindquarters, forcing it to turn, at times dragging two or three wolves with it. The wolves would break from the attack for 15-30 second intervals, and the bison faced them with its tail up.

Attacks from the rear continued from 1330 to 1350. At one time we noticed one wolf holding on to the bison's tail for about 10 seconds as the bison spun around, dragging the wolf with it through the willows. The bison appeared to be severely wounded and visibly tiring, although it did not go down at any time. At 1350, all animals were panting heavily; several of the wolves lay down while the bison stood facing the rest in a dense willow stand. Some of the wolves were covered with blood around the muzzle and neck, and the bison seemed to be bleeding profusely from the rump and flanks. By 1400, the bull went down and we proceeded to capture three members of the pack. The wolves were hesitant to leave the bison, but were manoeuvred into the open and darted within 30 minutes. The wolves fed on the carcass from 19-24 February."

Single wolves are capable of killing solitary bison under circumstances similar to those described for a single wolf killing a lone bull muskox (Gray 1970). In one case we located a single wolf feeding on a fresh carcass of an adult bull, but we could not determine whether it had been killed or had died prior to being found by the wolf. A local trapper (D. Dragon, pers. comm.) reported an incident of a single wolf following the tracks of a single bison for over 20 km along a roadway before he found the wolf feeding on the fresh carcass of an adult bull. Because the condition

of these bison was not known, it is conceivable that the wolves did not actually kill the bison, and may have come upon the carcass after the bison died of other causes.

A variety of physical infirmities in bison killed by wolves were documented. These and other debilitating factors, such as tuberculosis may have been present, but which we were not able to accurately diagnose from wolf kills that were in advanced stages of utilization.

2. *Summer Predation*

A. *Methods*

Data on food habits of wolves in summer were obtained from scat samples collected at dens and rendezvous sites, and roadways and trails. Trails were searched at 2-6 week intervals in the summers 1979 and 1980. Scats collected at home sites of packs were dated to period of known occupancy. Scats for which accurate deposition dates were not available were included in one of six categories, early summer (May - June), midsummer (July - August), late summer (September - October), early winter (November - December), midwinter (January - February), and late winter (March - April).

Hair samples in scats were identified by gross examination and comparison to known materials, as well as microscopic examination of hair medullae and scale pattern (Adorjan and Kolenosky 1969, Kennedy and Carbyn 1981). In cases where multiple food items occurred in the same scat, food items were expressed as a percentage occurrence of total remains recovered from the scat samples.

Relative biomass and number of different species in the diet were calculated by means of a linear regression developed by Floyd et al. (1978). Figures for biomass values in both summer and winter were derived from the winter sex and age ratio of bison killed by collared wolf packs, because it was impossible to distinguish bison calf hair from that of adults at certain times of the year.

Summer predation on calves was studied by following bison herds. The habituation process involved has been outlined in the introduction. These studies provided information on calf production, wolf predation and survival of yearlings through the first year of life. In summer, the effects of predation were studied by obtaining late spring/early summer cow-calf ratios, observing wolf/bison interactions, and at times witnessing wolves attacking and killing bison calves. Actual observations of kills were quite rare. More often it was possible to determine whether a calf was killed by watching the behaviour of cows. Cows that lost their calves paced restlessly back and forth over long distances, frequently returning to the area where the calf was lost. Cows exhibiting this behaviour often led to the location where the calf was killed. Remains of what was left varied from almost nothing to whole portions of calves.

Observations of wolf predation on bison were made from 1985 to 1991; with most systematic observations occurring in late May, early June, and again early October 1989, 1990, and 1991. At the same time, classified counts were conducted

to evaluate calf production and loss of calves in the first 4 months of life. Ground counts for spring 1989 were excluded because of small sample size (Table 55). In 1989 and 1991 observations extended over longer periods and were carried out for each spring (late May to early June) and fall (late September to early October). Total number of days in the field was 116. The technique was to follow herds and observe wolf/bison interactions at close range. When approached with care, bison herds allowed human observer(s) to follow them with minimal disturbance, to within short distances. Wolves spend a lot of time in association with the herds, and the observer had to be patient in order to allow both bison and wolves to accept the presence of humans. Patience meant watching herds at a distance, approaching them slowly under cover, or more often waiting in areas to which the herds would move. Classified counts were transcribed onto a tape recorder.

Results from the classified counts were compared with segregation counts conducted by Park wardens. The wardens conducted segregated ground counts, methods which were first developed by Cormack Gates, for bison in the Mackenzie Bison Sanctuary. The technique involves herding bison with a helicopter. A light helicopter was used because of greater manoeuvrability and they made less sound than larger machines. As much as possible, natural segregation of herds was used to locate drop-off points for the observers. The helicopter dropped off individuals about 1 km from the herd. The helicopter then circled around the edge of the herd. By moving up and down, the pilot could control the speed of bison movement, and by moving side to side, he could control the direction. The objective was to move the herd single-file past the ground observers. Bison were classified as to bulls, cows, yearlings, and calves.

Table 55. Summary of the time spent in the field 1985-1991 in calving range of bison in Area II.

Year	Number of Days	Dates
1985	6	21-27 August
1986	3	17-20 June
1987	14	29 May - 12 June
1988	6	19-25 June
1989	43	6-19 March; 29 May - 19 June; 27 Sept. - 7 Oct.
1990	18	18-24 June; 21 Sept. - 3 Oct.
1991	26	3-19 June; 27 Sept. - 6 Oct.
Total to date	116	

B. *Results and Discussion*

i) Scat analysis

Analysis of wolf scat data was based on percentage frequency occurrence of recovered food items in the scat samples, and on calculations of relative biomass and numbers of different prey species using a linear regression developed by Floyd et al. (1978). Volume of food items in each scat or relative estimated bulk (Fritts and Mech 1981) was not determined, however, multiple food items in one scat were uncommon. Differences between weighted frequencies (Carbyn 1980) and unweighted frequencies were not significant ($p > 0.05$). Total food items were considered an adequate representation of prey types as discrete components of scat samples, and were used synonymously in the biomass calculations.

It is important to note that all but one of the collections of scats pertain to non-Delta areas (i.e., Area I and at Lake One just south of the Peace River). In 1978, 105 scat samples were collected in the Delta area. Delta habitats provide a greater general availability of marshland species. Boreal forest environments have greater varieties of both forest and marshland species i.e., snowshoe hare, red squirrel, and also marshland species e.g., muskrat, beaver and waterfowl. However, in most studies of wolf food habits, it has been shown that the carnivore cannot subsist for longer periods of time on small mammals as the prey species.

Bison was generally the most important food of wolves in Wood Buffalo National Park in winter and summer, both in terms of frequency occurrence of food items (Table 56 and Table 57), and relative biomass consumed (Table 58). This confirms our results from radio-tracking data and ground observations. The occurrence of bison in winter scats was significantly higher ($p < 0.05$) than in summer, and the estimated relative bison biomass consumed was approximately four times greater in winter. Information for other areas containing bison exists only for the Slave River Lowlands, adjacent to the Park. There, bison frequency in scat samples was 51% in winter and 66% in summer (Van Camp 1987c). In that study bison comprised about 88% of total relative biomass consumed in winter, and about 70% in summer.

There was a significant decrease ($p < 0.05$) in occurrence of bison in scats between the summers of 1977 and 1978, and 1979 and 1980. The decrease may be partially due to a greater proportion of scats taken near wolf dens and rendezvous sites during the latter two summers (Table 59). The occurrence of small mammals, such as muskrat and snowshoe hare was higher at those sites from Area I. It is also possible that muskrat and hare populations increased substantially between those years, and were included in the wolves' diet in proportion to their abundance. Compared to previous summers, bison were conspicuously absent from Lake One during 1980 (Carbyn et al. 1981), the area from which most scat samples were collected during 1980.

Of the eight mammal species identified in the scat samples, moose ranked third in winter and fifth in summer in terms of frequency of occurrence. Biomass calculations indicated that after bison, moose contributed the greatest biomass consumed in both winter and summer. This was largely due to the estimated weight

Table 56. Percentage occurrence of food items in scats collected in summer (May to October) of each year from 1977 to 1980 in Wood Buffalo National Park.

Species	1977	1978	1979	1980	Total
Bison	29.3	19.6	7.2	10.8	13.3
Moose	0.9	2.4	2.8	2.1	2.3
Muskrat	15.4	15.5	34.6	42.4	29.8
Beaver	6.3	6.7	14.0	11.6	10.8
Snowshoe hare	13.6	37.1	28.6	20.5	26.5
Microtine	7.7	2.4	1.2	0.8	2.0
Porcupine		2.8	1.4	0.5	1.3
Squirrel	4.1		1.8	0.6	1.3
Waterfowl/grouse	11.8	9.5	5.4	6.8	7.3
Vegetation	9.5	2.4	1.3	0.2	2.0
Unidentified	1.4	1.6	4.7	3.6	3.3
Total food items	221	496	791	658	2166
Total scats	158	433	738	616	1945

Table 57. Percentage occurrence of food items in scats collected in winter (November to April) of each year from 1976-1977 to 1979-1980 in Wood Buffalo National Park.

Species	1976-77	1977-78	1978-79	1979-80	Total
Bison	53.8	48.1	53.2	60.8	54.9
Moose	3.1	8.6	9.3	10.4	9.2
Muskrat	23.1	12.3	6.2	2.2	6.6
Beaver	1.5	2.5	2.2	1.8	2.0
Snowshoe hare	4.6	19.8	21.8	12.9	18.1
Microtine	4.6		0.3	1.4	0.9
Porcupine			1.7	1.8	1.5
Squirrel			0.3		0.2
Waterfowl/grouse	1.5		0.3	1.4	0.7
Vegetation	7.7	8.6	2.7	0.4	2.8
Unidentified			2.0	6.8	3.0
Total food items	65	81	601	278	1025
Total scats	56	71	582	274	983

Table 58. Estimated relative biomass and numbers of mammalian prey consumed, as determined from frequency occurrence of food items in scats collected in winter and summer from 1977 to 1980 in Wood Buffalo National Park.

Species	Estimated weight of prey (kg)	Relative frequency of prey in scats	Relative biomass consumed[3]	Percent biomass consumed	Relative number of prey consumed	Ratios of prey consumed
Winter n = 1,025						
Bison	383.00[1]	54.9	441.40	82.4	1.15	1.00
Moose	425.00[2]	9.2	81.70	15.3	0.19	0.17
Muskrat	1.50	6.6	2.71	0.5	1.81	1.57
Beaver	12.50	2.0	1.26	0.2	0.11	0.10
Snowshoe hare	1.20	18.1	7.31	1.4	6.10	5.30
Microtine	0.04	0.9	0.34	0.1	8.56	7.44
Porcupine	10.00	1.5	0.87	0.2	0.09	0.08
Squirrel	0.30	0.2	0.08	0.0	0.10	0.09
Summer n = 2,166						
Bison	383.00	13.3	106.93	67.2	0.28	1.00
Moose	425.00	2.3	20.42	12.8	0.05	0.18
Muskrat	1.50	29.8	12.22	7.7	8.15	29.11
Beaver	12.50	10.8	6.80	4.3	0.54	1.93
Snowshoe hare	1.20	26.5	10.71	6.7	8.92	31.86
Microtine	0.04	2.0	0.76	0.5	19.04	68.00
Porcupine	10.00	1.3	0.75	0.5	0.08	0.29
Squirrel	0.30	1.3	0.51	0.3	0.64	2.29
Summer (adjusted values)		n = 2,166				
Bison	191.50[4]	13.3	55.60	56.9	0.29	1.00
Moose	212.50[4]	2.3	10.65	10.8	0.05	0.17
Muskrat	1.50	29.8	12.22	12.4	8.15	28.10
Beaver	12.50	10.8	6.80	6.9	0.54	1.86
Snowshoe hare	1.20	26.5	10.71	11.0	8.92	30.76
Microtine	0.04	2.0	0.76	0.8	19.04	65.70
Porcupine	10.00	1.3	0.75	0.8	0.08	0.28
Squirrel	0.30	1.3	0.51	0.5	0.64	2.21

[1] Based on known age ratio in winter kill of 8 adult males, 14 adult females, 17 calves and three yearlings with respective weights of 625, 470, 190 and 300 kg (H. Reynolds, pers com.).

[2] Based on known sex ratio in winter kill of one adult male: one adult female with respective weights of 500 and 350 kg.

[3] Floyd et al. (1978). Biomass consumed calculated from regression equation $Y = 0.38 + 0.02X$.

[4] Adjusted weights for bison and moose to reflect predation on young of the year.

of moose, which was based on the known kill ratio in winter (Table 58). With adjusted weights in summer, muskrat and snowshoe hare became more important.

Beaver occurrence in scats was low compared to other areas (Pimlott et al. 1969, Voigt et al. 1976, Peterson 1977), but as beaver hair can sometimes be difficult to differentiate from muskrat hair (Fuller and Keith 1980, Kennedy and Carbyn 1981), the importance of both beaver and muskrat remains unclear. Beaver was more common in summer than in winter scats (Tables 56, 57, 60, and 61) and the data indicated that this species was less frequent in late summer than in early and midsummer scats, then became more frequent in late winter (Table 61). Although the occurrence of beaver in winter scats was low (2.0% compared to 11% in summer), the greatest occurrence was in March-April (Table 61), when beavers possibly are more active and may therefore be vulnerable outside their dens. This situation was also documented in Algonquin Park (Pimlott et al. 1969); and sometimes occurs even in midwinter (Peterson 1977, Carbyn 1980).

Other small mammals comprised a minor portion of occurrences in wolf scats and relative prey biomass consumed, although microtines by virtue of their small size contributed the largest relative number of prey consumed. Ground observation of wolves revealed that quite often wolves would search out tussocks with interest and it is possible that they "playfully" pursue novel stimuli such as microtines. This is particularly the case for pups. Birds (waterfowl/grouse) were not included in biomass estimates because the regression equation is applicable to mammals only.

Examination of scats (adults and pups combined) collected at four denning localities and two rendezvous sites from 1978 to 1980 revealed considerable variation from year to year. As in the entire summer sample, muskrat occurrence in scats collected at Lake One dens and rendezvous sites increased from 1978 to 1980. With the exception of the Hornaday River den in 1978, muskrat was also an important summer food item at the other dens (Lake Claire 1978, Salt River 1979) and rendezvous site (Halfway Meadow 1979). Variation in bison occurrence in scats from dens and rendezvous sites likely reflects differences in bison abundance, particularly herds with calves in the vicinity of the home sites.

In summary, information from scat data indicated that ungulates (bison and moose together) comprised the bulk of the diet of wolves, in terms of relative biomass consumed (88% in winter; 70-80% in summer). Bison remains in wolf scat samples, ranged from 82% in winter to 57% in summer. Based on observations of wolf predation, the conclusion would be that the wolves' diet consisted entirely of bison, both in winter (from radio-collared wolves) and summer (ground observations). This bias in obtaining a different perspective on predation by large predators, depending on methods used, was also described by Mills (1992) for African carnivores. He described results obtained from direct observations and from radio-tracking and compared these with results from near-continuous tracking of collared animals for periods of up to 14 consecutive days. Using continuous tracking, he noted that diets reflected a larger percentage of smaller prey than previously documented. We fully concur with his observations.

Table 59. Percent frequency occurrence of food items in scat collected at dens and rendezvous sites from 1978 to 1980 in Wood Buffalo National Park.

Rendezvous sites	Hornaday River	Salt River	Lake Claire	Lake One			
Species	1978	1979	1978	1978	1979	1980	Mean
Bison	10.1	1.9	19.6	9.8	0.5	1.5	
Moose	6.0	7.6					
Muskrat	13.1	40.0	41.2	17.1	34.6	60.2	40.4
Beaver	5.4	29.5	13.7	14.6	4.9	15.5	9.4
Snowshoe hare	43.5	19.0	11.8	34.1	41.6	15.5	32.5
Microtine	0.6	1.9		7.3	1.1		1.5
Porcupine	2.4			7.3	1.1		1.5
Squirrel					3.2		1.8
Waterfowl/grouse	11.3		9.8	9.8	3.8	8.7	6.1
Vegetation	6.5		2.0		3.2		1.8
Unidentified	1.2		2.0		6.0		3.3
Total food items	168	105	51	41	185	103	329
Total scats	138	105	49	35	171	99	305

Table 59. Continued.

Rendezvous sites	Halfway meadow[1]	Lake One			
Species	**1979**	**1978**	**1979**	**1980**	**Mean**
Bison	2.1	20.7	22.6	3.6	9.4
Moose			2.2		0.4
Muskrat	57.4	8.6	19.4	48.3	37.9
Beaver	2.1	3.4	16.1	10.3	10.6
Snowshoe hare	6.4	34.5	23.7	19.5	22.1
Microtine		5.2	2.2	0.9	1.7
Porcupine	4.3	1.7		0.6	0.6
Squirrel			4.3	1.2	1.7
Waterfowl/grouse	19.1	13.8	2.2	9.1	7.9
Vegetation		10.3	3.2	0.3	2.5
Unidentified	6.4	1.7	4.3	5.6	5.2
Total food items	47	58	93	329	480
Total scats	38	44	86	297	427

[1] Occupied by the Lake Claire pack in 1979.

ii) Summer observations of wolf predation

Results of spring and fall classified counts indicated an average of 28 calves per 100 cows recorded in spring (Table 62). There was no statistically significant difference between the data collected by wardens and ground observers for the spring count. A similar comparison was not possible for the fall, as wardens did not collect fall data. Fall counts by L. Carbyn were 11, 17 and 21 calves per 100 cows ($\overline{X} = 16$), respectively for 1989, 1990 and 1991. Comparable declines over the first 4 months of the counts were 50%, 39% and 34% for an average of 44%. Comparable yearling counts per 100 cows were also recorded both in spring and in the fall. Yearling survival was an average of five calves per 100 cows from 1988 to 1991. Clearly yearling recruitment was low for the 1989 to 1991 period.

iii) Multiple kills

Prey populations existing in herds often are subjected to multiple kills when attacked by a wolf pack. Miller et. al (1985) found 34 caribou calves (*Rangifer tarandus groenlandicus*) killed by wolves in a 3 km^2 area. The calves appeared to have been killed within minutes of each other and about 24 hours before being found. Mech (1988) observed the killing of three musk-oxen calves in one attack sequence in the high arctic. In all of the above cases, size of calves were relatively small. We

Table 60. Percentage occurrence of food items in scat collected in early, mid, and late summer over the years 1977 to 1980 in Wood Buffalo National Park.

Species	Early summer (May-June)	Midsummer (July-August)	Late summer (September-October)
Bison	9.6	11.7	31.6
Moose	3.2	1.1	3.3
Muskrat	30.5	33.5	13.5
Beaver	11.3	12.6	3.3
Snowshoe hare	32.8	19.3	30.9
Microtine	0.8	2.7	3.6
Porcupine	1.5	1.3	0.7
Squirrel	0.9	2.0	0.4
Waterfowl/grouse	5.6	9.2	6.5
Vegetation	0.9	2.0	4.4
Unidentified	3.0	4.0	1.8
Total food items	930	966	274
Total scats	873	842	230

documented multiple kills of bison calves in early October, a time when calves weigh about 150 kg.

We noted a large pack of unknown number of wolves (possibly up to 26 wolves) frequenting an area around the north end of Lousy Creek. This pack specialized in multiple kills by first chasing herds with calves along a trail leading to a water crossing. After plunging through the water crossing, the herds would remain in a tight formation along trail leading through an aspen forest for another 250 m. The trail led out into an open meadow, but one branch of the trail paralleled the meadow. This physical feature was used to an advantage by the wolves. In full flights, a large portion of the herd would continue running along the trail, while some adults with calves would be pushed out straight ahead and into the open. The pack had perfected its hunting technique by quickly rushing out into the open and killing in multiples those calves that were together in close proximity. In one session, the pack killed three calves, consumed all but the skull caps and lower jaws with cheek teeth. Another two calves were killed in a similar fashion within a 5-day period. All kill remains were within 40 m of each other. Because bones were likely not completely formed and the calves were still nursing, both bones (with exception of the portion with teeth) and the stomach were completely consumed. Skull caps, and a few remaining bone chips was all that remained.

Table 61. Percentage occurrence of food items in scat collected in early, mid, and late winter over the years 1977 to 1980 in Wood Buffalo National Park.

Species	Early winter (November-December)	Midwinter (January-February)	Late winter (March-April)
Bison	62.8	62.2	48.6
Moose	7.4	14.1	6.7
Muskrat	4.1	2.2	9.9
Beaver	0.7	0.6	3.2
Snowshoe hare	14.2	12.5	22.7
Microtine	0.7	0.3	1.3
Porcupine		1.9	1.6
Squirrel		0.3	0.2
Waterfowl/grouse			1.3
Vegetation	6.8	1.6	2.5
Unidentified	3.4	4.4	2.2
Total food items	148	320	556
Total scats	140	311	528

Table 62. Summary of classified counts carried out by wardens and L. Carbyn from 1989 to 1991 in spring (late May/early June) and fall (late September/early October).

	Winter Pop Aerial Surveys		Classified Counts							Anomalies					
										Calves		Stub Tails		Diseased	
Dates	Area II	Total Park Pop	Cows	Calves	Ylgs	Bulls	Total	Calves /100 Cows	Ylgs /100 Cows	Red In Fall	Injury	Cows	Bulls	Cows	Bulls
1989 Spring															
Wardens	2093	3254	1050	226	37	505	1818	22	4						
1989 Fall															
L.C.			376	42	13	30	461	11	3	2/42		6/376	1/30	4/376	1/30
1990 Spring															
Wardens	1801	3375	854	258	31	191	1334	30	4						
L.C.	1801	3375	739	208	22	33	1002	28	3			9/739	0/33	8/739	0/33
1990 Fall															
L.C.			450	76	8	47	581	17	2	6/76	5/76	10/450	2/47	2/450	1/47
1991 Spring															
Wardens	1746	3310	734	225	50	214	1223	31	7						
L.C.	1746	3310	487	158	43	55	743	32	9		3/158	8/487	2/55	5/487	6/55
1991 Fall															
L.C.			272	57	13	22	364	21	5	1/57	1/57	1/272	0/22	1/272	0/22

3. *Impact of Wolf Predation on Bison Population Dynamics*

A. *Hornaday River Pack Model*

The impact of predation by the Hornaday River pack on bison was assessed by relating the proportion of bison killed by the pack over winters 1978-1979 to 1980-1981 to recruitment to the bison sub-population north of the Peace River (Table 63). Bison availability within the Hornaday River pack's home range was determined from an annual midwinter total count conducted by the Park Warden Service and from specific surveys flown on the predator/prey project. Comparison of over-winter calf survival on the Hornaday River pack home range, to recruitment over the entire primary bison ranges indicated that calf survival to April, north of the Peace River, in 1979, 1980, and 1981 was consistently lower than that calculated for the entire primary bison ranges.

As bison availability and herd composition within the home range of the Hornaday River pack varied within winters and between years, an effort was made

Table 63. Number of available bison, and bison killed by the Hornaday River pack in winters 1978-79 to 1980-81, Wood Buffalo National Park.

	1978-79	1979-80	1980-81	Total
Mean pack size	10	12	8	($\overline{X}$ = 10)
Available prey[1]				
Calves	5	30	57	92
Adults	174	457	656	1287
Bison killed[2]				
Calves	0	16	9	25
Adults	23	16	13	52
Percent killed				
Calves	0.0	53.3	15.8	27.2
Adults	13.2	3.5	2.0	4.0
Recruitment of new yearlings (%)[3]	9.7	5.4	8.3	($\overline{X}$ = 7.8)

[1] Based on midwinter total count within the Hornaday River pack's home range: 1978-79 - Hay Camp and Darough Creek meadows; 1979-80 - Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows; 1980-81 - Raup Lake, Hay Camp, and Darough Creek meadows.

[2] Based on predation rate calculated.

[3] Extrapolated proportion of new yearling over entire primary bison ranges, based on mean monthly decreases over first year of life (1978-1981 data).

to predict the impact of wolf predation on the bison population over the entire primary bison ranges. This approach was considered to be more accurate since it eliminated the effect of bison distribution, and facilitated the use of total counts and calf survival for the entire bison population on the primary ranges.

The population trend of bison on the primary ranges of Wood Buffalo National Park from 1978 to 1981 was calculated from three-year mean values of calf production, calf survival, and estimated adult mortality (Table 64). Observed values for calf proportions, and values for adult mortality which best fit the annual midwinter aerial counts, as described similarly for models of Alaska caribou populations (Doerr 1980), were entered at various intervals during the year.

The starting population size was based on estimated total bison numbers from the 1978 midwinter count. Estimates of total bison numbers in the Park, based on aerial surveys by the Warden Service were generally considered to be approximately 90% of the actual population, thus the population figures used in this model are greater than the values from the aerial surveys. The midwinter count for 1981; however, was in the opinion of D. Anions considered the most accurate on record, and the adult mortality rate for winter 1980-1981 was set to reflect agreement between our calculated population figure and the midwinter count.

Table 64. Composite one-year model of bison demography on primary ranges of Wood Buffalo National Park, 1978-1981.

		Adults[1]	Calves	Population size
Population estimate (30 April)				4575
Calf proportion:	May(16.0%)	4575	750(+750)	5325
	Aug. (13.4%)	4575	714(- 36)	5289
Adult mortality:	May-Oct. (2.5%)	4460(-115)	714	5174
Calf proportion:	Nov. (10.5%)	4460	524(-190)	4984
Adult mortality:	Nov.-Feb. (3.3%)	4311(-149)	524	4835
Calf proportion:	Feb. (8.9%)	4311	421(-103)	4732
Adult mortality:	Mar.-Apr. (3.3%)	4167(-144)	421	4588
Calf proportion:	Apr. (7.8%)	4167	353(- 68)	4520

[1] Bison older than one year.

Adult bison mortality on the primary bison ranges of Wood Buffalo National Park, as derived from the three-year means of productivity and survival (Table 64), was 414 animals while recruitment was 363, resulting in an overall decline of 51 bison. If the estimated adult mortality rates, and calf production and survival determined from aerial surveys are accurate, then the large number of adult bison, and the small number of calves (due to low availability) that died in winter 1978-1979 (Table 65) are consistent with observations of wolf predation on these age groups that year.

The proportion of bison killed by wolves on the primary bison ranges of Wood Buffalo National Park (Table 65) was based on the observed predation rates and prey selection by the Hornaday River pack in winters 1978-1979, 1979-1980, and 1980-1981, and by biomass consumption derived from 1977-1980 pooled summer scat data. Numbers of bison killed in winter were extrapolated over 180 days (November-April), and assumed a wolf population of 110 on the primary bison ranges. Summer kills were calculated from the estimated mean daily requirement by wild wolves of 1.7 kg per day per wolf (Mech 1977) over 185 days (May-October), as consumed by 110 wolves (adults and pups).

Given 34,595 kg of edible food was needed to sustain the 110 wolves in summer, 67% of which consisted of bison (Table 58), and 80% of any bison was edible (Pimlott 1967, Mills 1990), then bison biomass consumed in summer was 27,897 kg. Assuming age selection in summer was the same as in winter (1.47 adult:1 calf), and using weights of 465 kg for adults and 190 kg for calves, 110 wolves killed 47 adult bison and 32 calves in summer.

A comparison of recruitment and proportion of adult bison killed during 1978-1981 by wolves (Table 66) indicated that wolf predation of adult bison in some years may have nearly equalled recruitment, if mortality from wolf predation was assumed to be totally additive. Although much of the earlier literature implied that wolf predation was largely compensatory (Pimlott 1967, Pimlott et al. 1969, Mech and Frenzel 1971), this concept is changing. More recent studies indicate that wolf predation may at least be partially additive to other sources of mortality, and in combination with severe winters, disease, and decreasing forage for ungulates, can effectively limit the growth of, or reduce ungulate populations (Seip 1992).

To further elucidate the potential impact of wolf predation, bison mortality was examined by varying wolf numbers on the bison ranges, as well as levels of additive mortality, including those based on physical condition of bison (Table 67). The number of bison killed by wolves was calculated for estimates of 84, 110, and 136 wolves, and wolf predation was considered either 0% additive, 100% additive, or 58% additive for calves and 70% additive for adult bison. Recruitment and adult losses were calculated in the absence of wolf predation, to demonstrate the potential growth of the bison population when additive predation-mortality was removed.

Winter kills were extrapolated from predation rates and prey selection during 1979-1980 and 1980-1981 only, as winter kills by the Hornaday River pack were felt to be biased toward adult bison in 1978-1979, and probably did not reflect predation patterns over the rest of the primary bison ranges. Bone marrow analysis

Table 65. Estimated bison mortality, and number of bison killed by wolves on primary bison ranges of Wood Buffalo National Park, 1978 to 1981.

	Number of bison died[1]			Number of bison killed by wolves[2]		
	1978-79	1979-80	1980-81	1978-79	1979-80	1980-81
Adults						
Summer	117	114	112	47	47	47
Winter	445	219	217	248	145	177
Total	562	323	329	295	192	224
Calves						
Summer	265	84	329	32	32	32
Winter	99	187	225	0	145	133
Total	364	261	564	32	177	165
Total bison						
Summer	382	198	441	79	79	79
Winter	544	406	442	248	290	310
Total	926	604	883	327	369	389

[1] Adult mortality based on arbitrary rates: 1978-79 - summer 2.5%, winter 10%; 1979-80 - summer 2.5%, winter 5%. Calf mortality based on aerial survey results.

[2] Summer predation rates based on biomass consumed as per 1977-1980 pooled scat data, and projected for estimated wolf population of 110 and 1.7 kg/day/wolf requirement (Mech 1977) over 185 days. Winter kills based on projected predation rates (Table 42) applied to 110 wolves.

Table 66. Annual recruitment of yearlings and adult bison killed by wolves[1] on primary bison ranges of Wood Buffalo National Park, 1978-1981.

Year	Population size	Adult bison killed	Recruitment
1978	4685	295 (6.3)[2]	479 (10.2)[2]
1979	4565	192 (4.2)	443 (9.7)
1980	4474	224 (5.0)	242 (5.4)
1981	4522	—	375 (8.3)

[1] Based on food requirements and predation rates of 110 wolves, assuming predation is 100% additive.

[2] Proportions in brackets.

Table 67. Bison mortality, and effects of wolf predation on annual bison population growth in Wood Buffalo National Park, 1978-1981.

	Bison numbers[1]	Predation present								
		Predation mortality 0% additive			Predation mortality 58, 70% additive[2]			Predation mortality 100% additive		
Wolf numbers[3]		84	110	136	84	110	136	84	110	136
Calf mortality[4]	532	0	0	0	75	100	123	130	171	212
Adult mortality[4]	414	0	0	0	111	146	181	159	208	257
		Predation removed								
Recruitment	363	363	363	363	438	463	486	493	534	575
Adult losses	414	414	414	414	303	268	233	255	206	157
Population growth		-51	-51	-51	+135	+195	+253	+238	+328	+418

[1] Based on estimate of 4,685 adult bison, production of 895 calves, adult bison losses of 414, and recruitment of 363 bison (See Table 65 for details).

[2] Based on marrow-fat proportion of 0.8 for bison calves, where 58% of kills were above that value and considered additive mortality; for adults additive threshold was considered 0.7, and 70% of adult kills exhibited marrow-fat values greater than this.

[3] Population estimates on primary bison ranges.

[4] Based on mean of 1979-1980 and 1980-1981 observed predation rates by the Hornaday River pack (winter), and biomass consumed as per 1977-1980 pooled scat data (summer).

of bison calves killed in winter by wolves indicated that 58% had fat:water ratios greater than 0.80, and this percentage was used to determine calf numbers which were likely to survive in the absence of wolf predation (R. Peterson, pers. comm.). Similarly 70% of wolf-killed adult bison exceeded marrow-fat values of 0.70, considered critical for their survival without wolf predation.

Assuming that: i) wolf predation was at least partially, or perhaps totally additive mortality on bison, ii) wolf population estimates ranged between 84 and 136, iii) bison population parameters were reasonably accurate, and iv) predation patterns by the Hornaday River pack were typical of wolves on the primary bison ranges, wolves in Wood Buffalo National Park killed 14% to 40% of calves and 27% to 62% of adults that died each year (Table 67). Removal of the effects of wolf predation resulted in a reduction in adult mortality ranging from 111 to 257 bison, an increase in recruitment ranging from 75 to 212 bison, and a reversal from negative growth of -51 to positive growth ranging from +135 to +418 bison.

An underlying assumption of this potential population increase was that there were no limits imposed by habitat and available forage, and that wolves played no

part in reducing the occurrence of infectious diseases in the Park bison population. Caughley (1970, 1976, 1979) considered forage availability in relation to ungulate density as the prime factor in ungulate population regulation and felt that predators were incapable of preventing eruptions of ungulates. Cole (1971) postulated that ungulate populations in the U.S. Rocky Mountain National Parks were regulated by a combination of intraspecific competition and periodic severe weather, which affected forage availability. Similarly, continuing research on elk in Yellowstone National Park (Houston 1976) supports the hypothesis presented by Cole.

Contradictory evidence, however, was presented by Bergerud (1980) and Bergerud and Ballard (1988). They implied that for caribou at least, range deterioration (reduction of forage availability) was not implicated in population declines, and predation (human and natural) was considered the chief limiting factor to population growth. Keith (1974, 1983) and Fuller (1990) held the view that wolf abundance was primarily determined by the per capita biomass of their ungulate food supply, and wolf predation on ungulates was largely additive to other sources of mortality.

Forage availability on bison ranges in the Slave River Lowlands, immediately north of Wood Buffalo National Park, was not considered limiting to bison population growth (Reynolds 1974). In the apparent absence of wolf predation until 1987/88 (A. Look, pers. comm.) and an abundant food supply in a unused range apparently resulted in the dramatic growth of the introduced bison population in the Mackenzie Bison Sanctuary (approximately 100 km northwest of the Park).

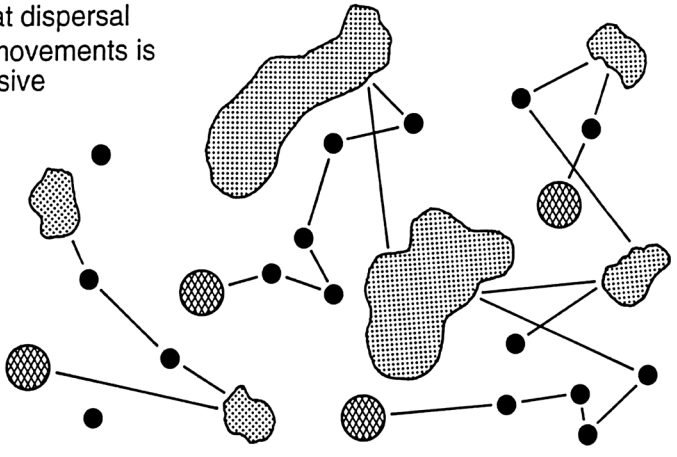
No evidence exists at present which links preferential wolf predation with diseased bison in the Park, although wolves are known to scavenge diseased carcasses. We do not know to what extent wolf predation reduces incidence of disease or how it may aid in the spread of infectious disease outbreaks in bison. We do know that brucellosis has been linked with lowered reproductive potential in other bovids, and as such its effects may be manifested in the relatively lower calf production (20-50% versus expected 60-75%) of bison observed in the Wood Buffalo National Park. We believe that during 1978-1981, the bison population in the primary bison ranges of Wood Buffalo National Park annually lost approximately equal proportions of calves and adults, and recruited yearlings at a rate of about 7.8%. The important point to highlight is that the calculations, based on the Hornaday River pack data, were made from a system with a more dispersed prey base (Area I), and no decline in numbers, than is the case for the Delta (Area II) — see Figure 50. We consider that 110 wolves is a conservative estimate of the number of wolves that were present on the primary bison ranges during that period of study and that these wolves were annually responsible for the death of at least 100 calves, and 131 adult bison, the remainder (296 calves and 277 adults) likely may have been killed by wolves or died of other causes. Wolf populations in 1978-1981 were not as high as in the earlier years (early 1970s), or as in the late 1980s and early 1990s. Overall impact of wolf predation would be higher in years of greater wolf numbers. As the bison population declined wolf predation will have an increasingly greater impact until they reach a level of diminishing returns. This is discussed in the next model.

Foraging Strategy

Hypothetical model of wolf movements in Areas I and II

Area I

– habitat dispersal
– wolf movements is extensive



Area II

– habitat concentrated in the delta
– wolf movements restricted to smaller area

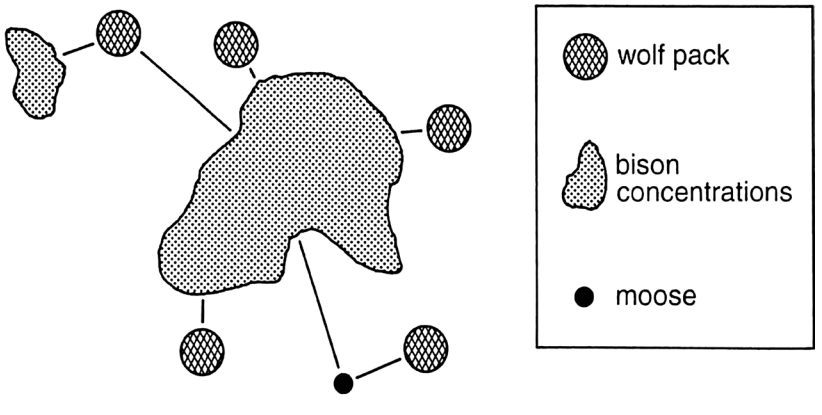


Figure 50. Two possible models in Areas I and II showing the differences in wolf/bison distribution in relation to association with habitat dispersion. High bison concentration in Area II results in more predictable availability of energy sources for the predator, and therefore, reduced searching time.

B. *The 1990s Model*

In 10-years (1981-1991), the bison population of Wood Buffalo National Park had declined by 41% (5,600 to 3,300). The wolf population on primary ranges increased from an estimated 110-130 to an estimated 165 (150-180) wolves (10 to 11 packs with average pack size of 14-17 wolves per pack), so that predator-prey ratios in 1991 were considerably altered from that in 1981. Furthermore, a major drying of the Delta had occurred. The results of one study (Jaques 1990) indicted that from 1976 to 1989, productive vegetation communities had decreased by about 47%, further changing the available habitat in that span of time. The 1990 model incorporates a combination of information from earlier predation rates, and the increase in wolf population. The model is broken down into a winter and a summer component.

i) Winter

The Hornaday River pack model relied on a combination of scat analyses on bison-calf production and survival, while for the 1990 model we relied on observations of predation in early summer (May/June), on observations of calf survival in the first 4 months of life, and on calf over-winter survival (Table 62, see details in earlier discussions). Winter predation rates for the 1990 model are the same as those used in the Hornaday River pack model.

The consumption rates for wolves used in the 1990 model are summarized in Table 68. Predation in winter (radio-tracking results) was directed toward all age classes of bison. In 285 contact days, (number of days that a radio-collared pack was monitored during 1979-1981), a pack of about 10 wolves (size varied over time) killed on average, one animal every 6.8 days. Food intake calculated for packs feeding on bison carcasses in winter varied from an estimated high of 6.4 kg per wolf per day to a low of 2.5 kg per wolf per day, with an average of about 4.3 kg per wolf per day (S. Oosenbrug, unpubl. report). For the 1990 model, we used the 2.5 kg rate.

Although it was noted that from four to six wolf packs ranged north of the Peace River, at least one of them ranged into secondary bison ranges. Therefore, calculation of the impact on bison herds for winter predation was based on conservative figures, by assuming that the primary bison ranges on Area I were occupied by only four major packs. The range of each of these packs also overlapped primary and secondary bison range. South of the river, we estimated that six packs occurred within primary winter bison ranges (see Figure 36).

Upper limits of weights of bulls and cows was 800 kg and 500 kg respectively (Reynolds et al. 1982). The weights of calves and yearlings vary with age. McHugh (1972) noted that calves at birth weigh from 14-18 kg. Seven-month-old calves weigh from 140 kg to 230 kg, and 12-month calves from 230 kg to 318 kg (H. Reynolds, pers. comm.). A figure of 300 kg was used for a long yearling weight. Overall weights were estimated at 625 kg (adult males), 475 kg (adult females), 300 kg (yearlings), and 190 kg (calves in winter). For purposes of calculations, we

Table 68. Kill rate calculations for wolves preying on bison in Wood Buffalo National Park (1990s model). Estimated food intakes per wolf set at 1.7 kg/day in summer and 2.5 kg/day in winter.

	WINTER		
	Daily/Monthly Requirement		Loss of
	Total	No. bison	bison in 180 days
First calculation			
Estim. pop. of 150 wolves (10 packs) - 2.5 kg/wolf/day	375 kg/day[1]	1.2/day[2]	216
			$\bar{X}$=240
Second calculation			
Estim. pop. based on 10 packs - radio tracking data	1 kill/6.8 days	4.4/month	264
			Average = 240 bison

	SUMMER		
	Daily/Monthly Requirement		Loss of
	Total	No. bison	bison in 180 days
First calculation			
Estim. pop. of 10 packs or 80 wolves - 1.7 kg/wolf/day	136 kg/day or 109 kg (adjusted)	28/pack/ 6 months[3]	280 calves
Second calculation			
Estim. pop. based 6 packs in Area II	16 calves/month/ pack	0.5 calf/pack/ day	576 calves (16×6×6)
Estim. pop. of 4 packs in Area I	4 calves/month/ pack	0.13 calf/pack/ day	96 calves (4×4×6)
			Average = $\frac{280 + 672}{2}$ = 476

[1] 150 wolves @ 2.5 kg per wolf per day equals 375 kg.

[2] 400 kg average weight per kill, minus 20% wastage equals 320 kg of food per kill.

[3] 1.7 kg of food per adult/subadult wolf, given 80 wolves equals 136 kg per day, minus 20% to account for non-bison prey equals 109 kg per day.

used an average of 400 kg for all bison. For slaughtering purposes to obtain meat for human consumption, the bison dress out at 55% (Fuller, pers. comm.). Percentage of inedible parts (horns, bones, parts of the hide, stomach contents) has been estimated at 20-30% of live weight for large ungulates. Therefore, 80% of 400 kg results in approximately 320 kg of edible meat per kill. One hundred and fifty wolves require about 375 kg per day, each kill provides a pack with approximately 320 kg; therefore, a minimum 1.2 bison are killed each day in winter (Table 68).

The estimated kill rate in winter, using these figures, is 216 bison, compared with our earlier Hornaday model, which estimated a kill of 130 adult bison and 100 calves in winter. Using the observed kill rate from the Hornaday River pack of one bison every 6.8 days, a pack of 10 wolves would kill 4.4 bison per month. Ten packs would kill 10 X 4.4 X 6 or 264 bison in 6 months. The mean of these two estimates is 240 bison per winter. These calculations are considered conservative.

ii) Summer

Food consumption by wolves in summer is considered to be lower than in winter. One figure is an estimated 1.7 kg per wolf per day (Mech 1970). Packs are also smaller. A pack of eight adult and subadult wolves would require an estimated minimum of 13.6 kg of food per day or 136 kg for 10 packs. Over the summer, that would result in 2,448 kg (minus 20% to account for other prey), or 1,959 kg per pack. Consumption of calves from May to October is virtually 100%. At a weight of 70 kg per calf, each pack would kill 28 calves (this is considered a conservative estimate). Ten packs would thus kill 280 calves in 6 months, or about 47 calves per month. Conclusions based on ground observation resulted in much higher estimates. During one 8-day period of monitoring of one pack (seven adults and subadults and undetermined number of pups) in June 1990, at least eight calves were killed. Actual kills in that period were observed on two occasions, and further evidence of predation was determined by watching the behaviour of cows after the loss of calves to predation (details described in an earlier chapter).

If bison are available, a pack of eight to ten wolves could readily kill, on average, one calf per day. In mid-to-late summer, larger calves provide increasingly more biomass per kill (field observations, L. Carbyn). Ground observations in early October 1991 revealed that in the Delta, one pack had killed three calves at one attack, and all but completely consumed the carcasses within 36 hours. What remained were small portions of the skull cap, lower jaws and a few bone chips.

Scat samples collected from 1978 to 1981 indicated that in summer other food items (up to 20%) are common. Beaver and muskrat numbers may have declined from 1981 to 1991 as a result of drying of the Delta, thus placing added predation pressures on bison, particularly the bison calf component.

We calculated kill rates based on observations (second calculation) separately, which resulted in higher rates than from food requirement calculations. A conservative kill rate south of the Peace River was estimated to be 16 calves per pack per month, and north of the river, four calves per month, resulting in a summer kill of 672 (576 + 96) calves for the total wolf population. Therefore, estimated calf losses varied from

280 to 672 for an average of 476 calves. Overall wolf kill was estimated at 716 bison per year (summer – 476 calves; plus winter adults and calves – 240).

Another calculation was used for summer mortality in which the kill rate per pack south of the Peace River (Delta area) was set at eight calves per pack per month. This resulted in a loss of 280 calves, and a total kill of 520 bison per year (280 + 240). Kill rate estimates per wolf (including calves, yearlings and adults) was about five bison per wolf per year based on a variable wolf population preying on the bison in the Park. The important point in these calculations is that calves were vulnerable to wolf predation, their biomass contribution was low, and the predation impact was high. Estimates of production, survival and recruitment rates were used to develop an iteration model.

iii) Iterations

An iteration model was based on the following: a bison population of 3,400 (1990 survey results) and an estimate of 6% of calves in March; the population of adults and yearlings was 3,196 (Area I – 1,504; Area II – 1,692). A sex ratio of 60 females to 40 males was the average observed sex ratio. This ratio is similar to the one quoted by Van Vuren (1983) although lower for females than observations in the Mackenzie Bison Sanctuary (Gates and Larter 1990). A population with 1,917 cows older than 2-years of age was the estimated reproductive component of the bison population in Wood Buffalo National Park in 1990. Comparable totals for Areas I and II, respectively, were 902 and 1,015. Given an estimate of 30 calves per 100 cows, production for the 3,400 bison in 1990 in Wood Buffalo National Park would be 575 calves per year (270 for Area I and 305 for Area II). If a higher estimate of 38 calves per 100 cows is used (compensating for calves not yet born in mid June and for those calves lost to wolf predation from early May to mid June), the total calf production per year would be 728 calves, and this total would be 1,269 at the anticipated 66 calves per 100 cows.

The estimated annual loss of 716 bison to wolf predation is not currently being replaced by production at 28 calves per 100 cows (575). These calculations indicate an annual deficit from 141 animals at a production rate of 30 calves per 100 cows, to a slight surplus of 12 animals at a production rate of 38 calves per 100 cows. There would be a surplus, if the lower summer kill rates were used. At production of 66 calves per 100 cows, the herds would produce 1,269 calves, and there would be a yearly surplus of 553 animals. The break-even point (to account for wolf predation only) is about 40 calves per 100 cows. However, because calves are most vulnerable, predation pressure on calves is not expected to be linear. Strong search image by wolf packs will continue as long as calves are available, the more calves there are, the longer the pressure on the calf component, and a switching to adult bison is only likely to occur as the calf percentage drops.

The observed low over-winter survival rate of three calves per 100 cows suggests that wolf predation on calves in winter continues to be high, and that recruitment does not offset the annual loss of adult bison. Given bison production potential versus predicted bison losses to wolves, we believe that wolf predation is

the immediate cause for the observed decline of bison in Wood Buffalo National Park. The question still remains whether the kill rate is abnormally high because the prey population is exposed to diseases. Such was apparently the case for increased lion predation on wildebeest in Etosha National Park (Berry 1981), where disease gave the predator an edge that it would normally not have if the prey were healthy. An argument against that, is that the bison in the north (Area I) and in the south (Area II) are diseased, and the only difference between the two areas is the drying of the Delta.

C. *Soper's Conclusions Re-examined*

One of Canada's foremost naturalists, J. Dewey Soper was commissioned in 1945 to evaluate the effect of wolf predation on bison in Wood Buffalo National Park (Soper 1945). After 4 months of field work (March to July, 1945), he concluded that "with a steady numerical increase (of wolves) since that time (1932), the picture has changed for the worse; the amount of predation has had a corresponding growth. The sum total of evidence now leaves no doubt as to an undesirable up-surge in the degree of wolf killing with moose and bison as principal victims in Wood Buffalo National Park." He further stated "Is there any good reason why wolves cannot be brought to a satisfactory numerical level? It seems to me to be unquestionably true that the bison should be protected against the slaughter by wolves." Soper was discussing wolf predation in relation to the need for native people to have less competition with wolves. Fuller and Novakowski (1955) were less direct with their evaluation of the impact wolves might have, but they referred to the wolves in the Park as a "menace".

The relationship between wolves, bison and the impact of wolf predation was not quantified by Soper, nor by Fuller and Novakowski. Soper spent time in the field and, as many native observers have concluded today, noted that evidence of wolf predation was everywhere and that the "losses" were significant.

We have concluded that Soper's observations, intuitive and dated as they were, were essentially correct in that wolves appear at times to have a significant impact on bison numbers. Native people who have commented on the impact of wolves on bison numbers have often come to similar conclusions. To increase the number of bison, Soper recommended predator control. He did this by stating that:

> "...these animals [wolves] are unquestionably increasing in numbers and are highly destructive of the wildlife resources of the park. It must be kept in mind that while Wood Buffalo Park is one of the national parks, it is not in the same category with other national parks which are maintained purely as wildlife sanctuaries and playgrounds for the people. Under circumstances governing parks of the latter type, I do personally adhere to the belief in a rational balance of nature where probably it would be found exceptionally necessary for man to interfere with the wildlife complex by "artificial" control.

> However, it must be agreed by all that Wood Buffalo Park is an entirely different proposition. Hundreds of Indian trappers are expected to be self-supporting on the game and fur resources of this area. In the very beginning, this introduces "man predation" on a large-scale and immediately cancels any possible functioning of the park in a true, natural condition, or with normal "balance of nature"..."

The "balance of nature" in the Park was affected by man's use of bison in the 1930s and 1940s for supply of meat to missions, and subsequently by large scale commercial slaughters, first carried out with the emphasis on disease control. The low kill by humans in the 1930s were of minor consequence in the dynamics of the bison populations. The 1950s were a transition period. Then in the 1960s and early 1970s, major roundup for anthrax control was a human factor that affected the bison population. Subsequent removal of human interference (both slaughters and predator control) resulted in the increases in wolves in the 1970s to 1990s and decreases in bison. The situation that bison find themselves in, in Wood Buffalo National Park would be alarming if maximum production of bison were to be an important management consideration. As a policy of resource management in national parks, ecosystem management programs place the emphasis on the system and not on sustained yield production.

We have examined Soper's observations from the mid 1940s. Soper described the impact of wolf predation in the system and reviewed the importance of the predator. We have provided preliminary quantitative data, and have come to similar conclusions regarding the importance of wolves in the population dynamics of bison. Our greatest confidence in concluding that predation is the major cause for the decline comes from two calculations. These are calculations of what bison losses are without wolves, and with the lower observed reproductive rates, and with wolves at variable reproduction rates. When this is applied to crude models the predictions support the observed events.

This analysis eliminates all but one of the hypotheses i.e., Hypothesis B, listed in the Introduction. Because, in thousands of hours of ground observations, and aerial observations, black bears were not observed to prey on bison, we can eliminate that predator from the equation. The only serious hypothesis still to be evaluated is hypothesis C and that is dealt with in the Discussion. The models have suggested that without wolf predation, there would be an immediate response; i.e., after the first calving season the population would increase and yearling recruitment would be much higher than is shown at three to four animals per 100 cows now recorded. Our conclusion, therefore, is basically the same as Soper's: that the bison population is affected by wolf predation. We believe that without wolf predation, and in the presence of diseases, the bison population would increase. In the final analysis, it is not calf production, but survival that is most important. With three to nine percent survival of calves to the yearling stage, recruitment does not offset the losses from adult predation, drowning, disease, and all other mortality factors acting on the population.

i) Prey and habitat dispersion

Figure 50 outlines a likely dispersion difference of habitats for Areas I and II. If prey distribution is dictated by habitat availability, then search patterns of wolves to find prey will differ between Areas I and II. A hypothetical example of how this search pattern could manifest itself is shown in the figure. We do not consider this as an accurate representation of the real situation; however, more work of a detailed nature is required to examine relationships of habitat to predator/prey distribution in the systems within Wood Buffalo National Park.

It was already mentioned that numerical changes in bison north of the Peace River (Area I) were such that the bison population from 1971 to 1991 (post predator control) essentially levelled off with only a slight decline, while the population in Area II (Delta) declined markedly. The greater productivity and concentration of suitable habitat for bison is within the Delta.

A closer examination of bison ranges north and south shows that in fact there are differences in:

a) effects of habitat losses in Area II because of the drying of the Delta (Jaques 1990).
b) distances and dispersion of major summer habitat north versus south of the river;
c) much greater concentrations (larger herds) south of the river, reflecting undoubtedly the more productive ranges in that area.

The dispersed habitat to the north results in a greater proportion of the bison in that region being on secondary ranges. Over a 20-year period approximately 91% of the winter distribution in Area II was on primary ranges while bison north of the river were more dispersed on both primary and secondary ranges. Furthermore, few moose have been seen in the Delta portion while they are commonly seen in the primary areas north of the Peace River. We believe this model to be worth testing. Effects of wolf predation on herd size needs to be studied (Heard 1992) as is the case with effects of wolf predation on diet shifts (Edwards 1983).

VIII Discussion

The exact causes and effects that led to the decline of bison in the last 20 years in Wood Buffalo National Park are difficult to establish in retrospect; however, a review of the events leading up to and during the decline provides a logical explanation of the current situation. In taking this approach we are fully cognizant of the shortcomings in attempting to understand complex processes within communities for which there likely are no simple answers. The bison, disease, wolf and habitat components are intertwined in a complex web and the connections, through evolutionary processes, difficult to discern. From our studies we believe that wolf predation is the single, most important factor causing the observed declines in the bison herds. However, predation does not operate in isolation. Coupled with predation is the loss of habitat in the Delta. We believe the rapid loss of habitat in the Delta has rendered the bison more exposed to wolf predation. Superimposed on this is that wolf control has virtually ceased over the 20-year period (only a few wolves are still killed annually by man). The most difficult problems hinge on being able to identify how important diseases are in rendering bison more vulnerable to wolf predation. However, disease likely is of the same importance in Areas I and II.

The dependent variables in this, as in other systems, are the distribution of species and their relative abundance (Diamond 1986). These dependent variables are controlled by sets of independent variables — environmental factors and other species.

We have to ask ourselves, what is the best way to study the interactions between these two sets of variables? Romesburg (1981) identified three scientific methods frequently applied, i.e., 1. induction, 2. retroduction, and 3. hypothetico — deductive methods. He noted that wildlife science uses the first and second methods, but almost never the third. Induction involves the use of repeated observations to uncover laws of association. In this study, field trips conducted in spring and fall from 1985 to 1991 were designed to obtain observations. In modern ecology such an approach is often scorned as being "non-scientific". Retroduction is defined as the "best guess hypothesis" to explain natural events. Romesburg (1981) pointed out that retroduction is not always worthwhile because it is possible to generate alternative hypotheses to explain any set of observations. This indeed

is the very danger we have run into in this study. Many northern residents have come to similar conclusions about the impact of wolves in the system and their response often is essentially as follows:

> "With all the abstract learning and academic "mumble jumble" it really boils down to a very simple equation. Predators kill prey, wolves eat calves, there are a lot of wolves out there, and the calves are being killed at a very high rate. Anyone who doubts the impact wolves have should go out and watch 26 wolves chase a herd and kill three calves in one session day after day for 365 days a year".

The "clincher" would be if those critics who fail to appreciate Occam's razor could be satisfied by being presented with a carefully designed experiment using the hypothetico-deductive method. This method involves setting up a hypothesis, deducing testable predictions, carrying out suitable tests and then using observations to decide whether the prediction is met. This ideal was not achievable because of limited resources and the Park's mandate, which generally precludes extensive manipulation of wildlife. We therefore come to Romesburg's objection — "I prefer conclusive over nonconclusive studies...saying here's how we did it; now here's how you can do it right" is simply not good enough. We have also run the risk of applying the "shotgun pattern approach" to the project. That is, we assembled a great deal of information (e.g., predation, hydrology, winter severity) without knowing how it might fit in, leaving the reader at the end asking — so what? We proceeded to explore all avenues and concluded that above all, wolf predation was the single most important direct cause for the observed and well documented decline of bison in Wood Buffalo National Park. The decline was not even for areas north and south of the Peace River. Construction of the Bennett Dam and filling of the Williston Reservoir undoubtably presents itself as a "natural experiment". This may well explain why bison north of the river remained essentially stable, while south of the river the decline was accentuated. Our general conclusion is that without wolves, both the bison populations north and south of the river would increase, with or without the dam. However, with the drying of the Delta, wolf predation has a much greater effect on bison numbers south of the river, than it has north of the river. The logic of our conclusions is based on a review of the historical events and empirical evidence obtained from 43 radio-collared wolves and 116 days spent living with bison and wolves in the bush. Therefore, we rest our case in what Platt (1964) called "strong inference" without being able to resort to experimentation.

A review of the logic is as follows. The bison population of Wood Buffalo National Park and surrounding area reached a peak sometime between 1940 and 1971. After 1970/71 they declined sharply. This was after a period following the predator control program that began in the mid 1930s, was most intense in the 1950s and was discontinued sometime in the mid-to-late 1960s. Wardens began monitoring the bison population during the early 1970s (when bison numbers were still relatively high), so their surveys quantified this decline. Wolf numbers were high

in the early 1970s. Bison declined rapidly in the early 1970s. During 1975 to 1985 wolf numbers declined from the previous four years. Between 1976 and 1988, the bison numbers were either stable or declining slowly; during 1989, another substantial drop in bison numbers was recorded. Wolves increased after 1989. This inverse relationship fits well except that bison numbers declined in 1984, prior to the wolf increase of 1989. The exponential model suggests an instantaneous rate of decline sustained throughout at minus 7% (-0.07), whereas north of the river there was no change. This graph is convincing and cannot be dismissed lightly (Fuller, pers. comm.). We have to review other factors as well. It can be argued that the bison population was artificially high prior to 1971 and that current numbers are at the level that would have prevailed if a large number of bison had not been introduced to the area in 1925-1928. It will never be known what the population might have been if bison numbers (and wolves) had not been manipulated.

During the late 1960s the bison numbers appeared to be down only slightly from previous years. What caused the more precipitous drop to the numbers recorded in 1975? The following factors can all be implicated in having contributed to the decline up to 1975:

1. The Bennett Dam was completed in 1968. Prior to that, floods that recharged the Delta and stimulated the growth of sedge meadows occurred, on average, once or twice every five years. Following construction of the dam, water levels in the Delta dropped. Low water levels resulted initially in an increase in what appeared to be suitable bison range; however, the quality of the ranges subsequently deteriorated (Cordes 1975; Jaques 1990, 1992).
2. Winters were moderate to severe during 1970/71 and 1971/72, but such variations were not much different from previous long-term averages.
3. Poisoning of wolves was officially discontinued in the 1950s, but wolf controls of various intensities continued into the 1960s. Numbers of wolves declined after the flood in 1974, but increased subsequently.
4. Anthrax roundups started in the 1960s. There was renewed emphasis, especially during 1972, on roundups for vaccination. This activity led to injury and death of bison.

All indications are that the combination of these factors are implicated in the decline of the Park's bison in Area II and stabilizing in Area I between 1969 and 1973.

The importance of their cumulative effect was subsequently overshadowed by one event that had catastrophic consequences. Extreme flooding of the Delta occurred during the spring of 1974, resulting in the mass drowning of bison. Figures are sketchy in the exact number that drowned, but aerial surveys of bison before and after 1974 indicate a probable loss of about 3,000. The water levels remained extremely high throughout the remainder of the year; still more bison drowned later

in the year (especially after the freeze-up of flooded meadows), and access to large areas of range was restricted for some time after (S. Cooper and S. Flett, pers. comm.).

This secondary input could have produced food stress in the population. Nutritional deficiencies in ungulates are known to produce the birth of stillborn young. In addition, if lack of suitable range produces stress, it may, in turn, have negative impacts on fertility. Caribou, for example, cease to reproduce when severely undernourished (Thomas 1982). Furthermore, calves born to nutritionally stressed cows may have a lower survival during the immediate post-partum period than do those born to a well-nourished animal. The result may be a decline in calf production and survival, which would eventually lead to inadequate recruitment. Nothing can currently be said about the extent to which the nutritional stresses may have affected the general vitality of the bison in Wood Buffalo National Park. Because there is no evidence that these bison are, or were, nutritionally stressed, this scenario is only presented as a theoretical possibility.

The cumulative effect of the extensive flooding was exacerbated by other factors. The large-scale roundups of about 28,000 animals for anthrax vaccination carried out from 1965 to 1977 displaced animals from their summer ranges, and disrupted animals during the sensitive calving period. It was clear that despite the cessation of anthrax vaccination programs and a series of relatively mild winters between 1976/77 and 1980/81, the Park's bison population did not recover to former levels after the disastrous drownings of 1974. We suggest that wolf predation had an important role in the population dynamics of the Park's bison during this period, because once the impact of the drownings and roundups had taken effect, predator/prey ratios, and thus predation on the remaining bison, increased. At lower prey densities and stable or increasing wolf densities, a greater proportion of the total bison population was killed in years after the flood than had previously been the case. Therefore, wolf predation had a proportionately greater impact after the flooding than it did before. In such a situation, the outcome would be governed by the efficiency of wolves, the vulnerability of bison, and the biological feedback systems governing population regulation mechanisms influencing the wolf population.

Winters were severe for the two years subsequent to the floods (especially during 1975/76). Bison may become more susceptible to harsh winter conditions by disease; in turn, disease, like harsh weather, may make bison more vulnerable to predation. Ungulate populations can rebound from periodic setbacks, if the factors that caused those setbacks are removed. This does not seem to have happened with the bison in Wood Buffalo National Park. Again, we come to the question: What has caused the failure of this population to increase? One explanation is that in the 1980s and 1990s the bison were in what population ecologists have referred to as a "predator pit". This is where predation has a major impact on prey numbers. In a sense, the concept of a predator pit is not applicable to systems where there are no alternate prey populations. Energy resources from smaller prey, such as muskrat, beaver, and snowshoe hare are considered minor in the ecology

of wolves generally (Mech 1970), even though summer scat samples indicate their presence in the diet of wolves. We have concluded that this is also the case for Wood Buffalo National Park.

The predator pit concept states that predators can regulate ungulate prey numbers at low densities, but not at high densities (Haber and Walters 1980). Factors consistent with a predator pit theory include long-term low density of a prey species, coupled with alternate prey availability. Declines of ungulates often are initiated by other factors. That is, wolves only cause the "pit" conditions because this mortality source interacts with other factors (in this case, habitat change). For example, Mech and Karns (1977) provided evidence that wolf predation caused deer populations to decline to low numbers in habitats that were changing to the disadvantage of deer foraging, and in the presence of severe winter conditions over a period of consecutive years. The impact of predation depends on the magnitude of losses to wolves compared to the potential recruitment of prey in the absence of predation (Seip 1992). If in the Wood Buffalo National Park system, diseases were responsible for the reduction in calf production from about 67 calves per 100 reproductively mature cows to 30-35 calves per 100 cows, then the potential recruitment in the absence of predation, or other mortality factors of similar intensity, of the diseased population would be about 20 to 30 calves per 100 cows. The observation, in the presence of wolf predation and disease, is survival of three to nine calves per 100 cows.

Wolves in Wood Buffalo National Park have a strong search image for calves. Bergerud (1980) noted that predation by carnivores can reduce caribou calf survival by 80%-90% although these samples may be biased as they could pertain to a segment of the ungulate population that is most exposed to predators. Peterson et al. (1984) calculated that moose in single ungulate prey systems accounted for up to 97% of ingested biomass. They calculated a mean of 3.9 calves killed in summer for every adult moose killed. In Alaska, moose calf survival to 5 months of age averaged 39% (1976-1986) (Ballard et al. 1991). Predation accounted for 83% of total mortality of neonates. They found that 96% of natural mortality occurred in the first 6 weeks of life, with brown bears accounting for 73%. In the absence of having seen adult bison being killed in summer, we believe wolves only rarely killed adults during these periods each year the studies were carried out. Wolves are generally considered to be opportunistic predators selecting those that are easiest to kill. We have not seen this to be the case for bison in Wood Buffalo National Park. The search image for calves is so strong that hunting wolves would often walk by obviously debilitated, even crippled adult bison, in favour of killing calves. This predation pressure on calves resulted in an estimated loss of about 50% of the calves from May to October, and a further 80% of the remaining calves to the following May. Added to the loss of calves is the predation of all age classes in winter. A relatively small pack in the Park (10-14 wolves) killed on average one bison (all age classes) every 6.8 days. We recognize that the Hornaday River pack and 1990s model lack in the coherence of a summer and winter data set. Obviously the challenge is to put in place a solid research program that will refine the data set,

and that will test the hypothesis that predation is an important proximate cause that accounts for the lack of recruitment of calves, and accounts for the observed decline of the bison population.

Our analysis of all the factors that may have contributed to the dramatic changes in bison numbers in Wood Buffalo National Park leads us to believe that wolf predation is the most obvious and immediate cause for the observed decline. What is more difficult to identify are the factors that predispose bison to wolf predation. On the surface it appears that habitat deterioration is the most obvious such factor. Disease and habitat deterioration may well be important contributory or ultimate factors. By setting up the original hypothesis (Hypothesis B) we also invoked the possibility of predation by another large predator.

Could black bear predation be important in the system? Recent studies in other areas of wolf/bear predation on moose and caribou, have shown that bears can remove a substantial number of calves during the calving period (Franzmann and Schwartz 1986, Ballard and Larsen 1987, Boertje et al. 1988, Larsen et al. 1989). Schwartz and Franzmann (1991) reported significant bear predation on moose calves from birth to age 30 days. Moose calves in that system provided a source of protein energy in spring when other foods were less available. We saw little evidence of black bear predation on bison and noted only two situations where it might have occurred. A large number of black bears (numbers were not recorded) were seen on one calving area in early summer in the Delta region one year (D. Huisman, pers. comm.). There were no ground observers there at the time to record if predation took place. On another occasion, Huisman observed one interaction where a black bear appeared to be harassing a herd, but in neither case, was there any evidence of persistent attacks that could have resulted in kills. On the other hand, as already discussed, wolf predation on bison calves was high. Van Ballenberghe (1987) suggested that predation on moose calves is likely additive, whereas predation on adults is more likely compensatory. We believe this may also apply to the wolf/bison system of Wood Buffalo National Park during the 1970s and 1980s.

Bison killed, both summer and winter, often appeared to be in "good" health. The latter is difficult to quantify, and therefore, such statements need to be qualified, but there were no obvious signs that debilitated bison were the specific targets of wolf predation or that those that were killed were less "healthy" than those that were not killed. It is certainly possible, for example, that tuberculosis, being a pulmonary disease, affects the ability of bison to escape when being chased by wolves.

A generality about predator-prey systems is that, through evolutionary processes, the predator and prey components co-exist in a roughly mutually beneficial relationship. To be successful the predator must be barely able to capture enough prey to survive and reproduce, and the prey must have at least an equal or better chance to escape. This means that the predator, under most situations, cannot quite match the defences of most members in a prey population. It can switch to other age classes of the same prey species or different species at different times of the

year. This deadlock may be broken if the prey in some way find itself in a more vulnerable situation. Such conditions could be the presence and location of water bodies, deep snow, poor health, rough terrain, age, obstacles that obstruct escape, and others. Theoretically, a co-evolved predator cannot quite match the defences of most individuals in a prey population (L.D. Mech, pers. comm.). The predator must hunt over a large area to find a potential victim. If diseased prey are available, the task may become much easier. This has led some to suggest that disease is the primary cause for the observed bison declines in Wood Buffalo National Park (Tessaro , presentation at FEARO panel hearings), and therefore it could be argued that disease is causing bison to be in a "predator pit".

Evidence against the disease hypothesis rests in the fact that bison numbers north and south of the Peace River have not changed synchronously, yet both populations are diseased. The population in the Delta is highly clumped in the productive sedge area. Loss of prime Delta habitat through effects of the Bennett Dam is likely further accelerating the "clumping" process. Predation success is less density-dependent if prey is found in predictable areas than would be the case in situations north of the river, where habitat and bison are more dispersed.

The wolf population of the Delta fluctuated through the 1970s and 1980s. The flooding in 1974 resulted in a decline in the wolf population. We speculate that denning by wolves was affected. Wolf numbers began to recover, but later in the decade prices for long-haired furs were high; wolves were heavily hunted and trapped, which resulted in further decreases in the population. The wolf population subsequently increased in the Delta so that the population in the early 1990s was high again. North of the river, wolf fluctuations are less well documented, but numbers appeared to be more stable.

We have concluded that predation, not disease, has caused the observed decline of bison in the Park. We want to stress, however, that we do not imply that disease is necessarily insignificant. Disease may be important in predisposing prey to predation. Calves for example, may appear to be perfectly healthy, but if cows are diseased, vulnerability of offspring to predation may be increased. On observing calves in the field, they appeared to be healthy, but we cannot be certain without further study. One source of evidence would be if we could evaluate effects on bison recruitment in the presence of disease, but in the absence of wolves. The other line of reasoning is to try to explain why bison numbers declined south of the Peace River (Area II), but not in Area I (north of the Peace River). All evidence indicates that disease is well established in both populations, therefore, we believe predation rather than disease, has been the cause for the different rates of decline. Our prediction is that if predation in the area north of the Peace River increased, bison numbers would decline there also.

We suggest that differences in dispersion of habitat between Areas I and II, and the resultant conspicuous concentrations of large bison herds in the Delta (Area II) have over the past 20-years made them more vulnerable to wolf predation. During the 1985 to 1991 summer field observations another potential antipredator strategy was noted which would aid in the protection of calves. It was repeatedly

observed that small herds (10 to 30 animals) generally contained higher ratios of calves than was the case for larger herds i.e., 30-200 animals. Small herds with calves were noticed to be very mobile. Therefore, by moving rapidly from small habitat patch to another, and not staying as large herds in one area, the young could be made less accessible to predators.

Disease undoubtedly contributed to the decline, but if mortality exceeds recruitment then any source of death, (even such a stochastic event as a bison being killed by a single lightning strike) will contribute to the decline. Loss of habitat (drying of the Delta) would increase the clumping effect and remove alternate prey, thus increasing predation pressures on the bison calves. In the absence of data on the nutritional state of bison in the Park, it is difficult to implicate habitat loss as a proximate cause for the decline. In the final analysis we believe the lack of recruitment of calves into the population to be the most relevant factor in the decline.

The progressive reduction in recruitment of calves into the population meant fewer calves surviving to adulthood, resulting in an increased reduction of the reproductive component of the population. This effect was cumulative. If losses through predation on calves were lower north of the river, this would in part balance the higher losses south of the river and provide the northern bison an added advantage of a higher reproductive potential. This could well explain why the Park's bison population tended to level out at approximately 5,000 during the early to mid 1980s. The elimination of roundups and the series of mild winters late in the 1970s may also have contributed to the stabilization of this population. However, by the mid 1980s, it was obvious that the number of bison was not increasing in response to more favourable conditions. The most readily discernible factor keeping numbers down appears to be relatively low recruitment of yearlings into the reproductive stage. Although disease may have caused low productivity and high non-predator-related mortality, we believe that the high loss of pre-reproductive-aged bison (calves) through wolf predation was primarily responsible for this situation. Predation on bison calves begins soon after birth. Findings to date (Carbyn and Trottier 1987, 1988) indicate that antipredator behaviour in bison is strong shortly after calves are born (May and June), so that the impact of predation can be less pronounced at this point than it is during winter. We believe that the situation described by Carbyn and Trottier (1988) — prolonged attacks without success — is common, yet persistent attacks on herds with calves invariably result in the loss of many calves. Maternal defences by cows may not be as strong during the rut. Regardless of when calves are lost the overall effect of predation on this age class is considered to be significant.

Recorded calf production was 28-35 calves per 100 cows in 1989, 1990, and 1991 higher than the recorded pregnancy rate of 22% (181 slaughtered cows from the Slave River Lowlands, Tessaro 1987). An overall pregnancy rate of 47% was recorded over several decades in the whole Park (see Table 20). A second source of information to suggest that current productivity is higher than the observed 30% comes from a review of calf losses. If a major proportion (50%) of the calves seen

in early June are lost to wolf predation by the end of September (12 week period), then it is not unreasonable to suggest that a good number of those initially born (possibly as high as 37 calves per 100 cows) i.e., the difference between 30 per 100 cows observed and 67 per 100 cows theoretical are killed by wolves before mid May/early June. If overall mortality rates in fact are low, then productivity is less important to population regulation than are calf survival and recruitment. The most startling findings shown by our results, and those of the warden surveys, reveal that since 1988, the herds in the Delta have contained less than five yearlings per 100 cows by mid June. In addition, both ground and aerial observations have shown that kill rates of bison of all age- and sex-classes were high in mid to late winter. In one observation we noted that in late March a pack of 26 wolves (or possibly a combination of two packs — 16 and 10, seen close together) killed three bison (two cows, one bull) in one 24-36 hour period. Evidence such as this leads us to believe that during the current decline, the bison population on the Delta is rapidly entering a classical situation of what has already been described as a "predator pit".

In an evolutionary context, one would expect bison to "resist" the long-term debilitating effects of both predation and disease. Tessaro (1987) found that 25% of 72 bison carcasses suitable for examination were infected with brucellosis, while 21% showed evidence of tuberculosis. These findings, in our view, raise the question of why these figures are so low, because it seems likely that animals in herds, which are in close, nearly continuous contact, would show much higher rates of infection. The possibility that bison in the Park may be developing resistance to these diseases has not been evaluated. Furthermore, it is possible that through natural selection, wolves are forcing bison through a "bottleneck", thereby reducing genetic variation. The possibility of extinction has been raised for other prey species in a "predator pit" (Seip 1989). We cannot predict what will happen to the bison in Wood Buffalo National Park if left to find their levels, without human manipulation. Certainly with current trends the population in the Delta portion south of the river could reach very low levels. Some increased shifts of predation pressures in other areas may well result over time. The Park is probably large enough so that, with minimal human interference, long-term evolutionary processes will enable the bison there to remain part of the ecosystem. However, if the impact of loss of habitat, predation, or disease increases in the future, the bison will have to evolve greater resistance to these factors to survive. Alternatively, in the case of predation, at some point the wolf population could be expected to drop as the prey population declines to a crucial level. Although one may not be justified in "crying wolf" if the low rate of recruitment in the bison population of Wood Buffalo National Park is the result of low productivity, high non-predator related mortality (i.e., such as disease), or both, it is likely that until the feedback mechanisms that affect wolf reproduction and survival become operative (thus allowing calf survival and recruitment to increase), the downward trend in this bison population can be expected to continue. Viewed in the setting of a national park, the decline of these herds is not necessarily disastrous. Whatever population is present should be viewed in the context of its ecological setting, i.e., the existing bison population is

regulated by the constraints placed on it by the biological and physical components of the system. Such a view that carnivores within ecological communities in national parks represents integral parts of the whole is widely held (Joubert 1991). However, there is a case in Kruger National Park, South Africa where lions (*Panthero leo*) can, in specific situations, be removed in limited numbers for case specific, clearly defined goals (Smuts 1978, Joubert 1991). This is a case of predator control to maintain biological diversity.

The current decline in the bison population should not detract attention from the much wider and potentially more disastrous ecosystem related problem. The long-term ecological collapse of major portions of the Delta (brought about by drying conditions resulting from the construction of the Bennett Dam) needs to be addressed (Townsend, pers. comm.). There is no doubt that flooding in the Delta has been affected by the Bennett Dam. Although weirs have helped to maintain water in the system longer than it would be if they were not present, they have not replaced the natural spring flooding followed by quick drawdown that is required to maintain bison range. Cordes and others (Cordes 1975; Cordes and Strong 1976; Cordes and Pearce 1977, 1978, 1979) provided baseline information on the condition of bison ranges in the Delta and documented changes in these ranges. Through modern techniques using LANDSAT Multispectral Scanner (MTS) imagery a more quantitative approach was possible to document change (Jaques 1990). Follow up ground truthing will be required and, we believe, that in the future, such information will be of great value in enabling investigators to quantify the rate of change in the habitats of bison and other wildlife species in the area. It is evident that the deterioration of the range caused by the lack of periodic flooding (which has remained infrequent throughout the 1970s and 1980s) is an ongoing process that has, and is, creating major problems with the bison range. Each year local residents report that progressively fewer extensive sedge meadows remain in the Delta, and that herds are keying in on these diminishing food supplies. If spring flooding and drawdowns are further impaired, ranges will continue to deteriorate and our generation will be handing down to future generations an impoverished park environment. Long-term corrective action is needed and so are careful studies of the potential immediate and long-term impacts that any human manipulation of the hydrological regime would have on the bison ranges and the environment generally. Speedy implementation is important, as irreversible processes may set in which will limit future options. Much has already been debated.

The proposal of a hydroelectric dam on the Slave River gave the issue a focus in the early 1980s. At that time, the potential impact of such a dam on the Delta was of major concern. Such a structure would not have solved the hydrological problems that were, or are currently, being experienced in the Delta, unless rapid drawdown could be assured each year to simulate the natural or quasi-natural conditions that are favourable to the retention of *Carex* meadows. On the basis of theoretical considerations, the solution probably more appropriately lies with the construction of an "ecological dam" on the Slave River (Townsend, pers. comm.), which could be used when required to produce flooding in the Delta. Such a

structure may be costly, but its design would allow for restoration of the Delta's hydrological regime so that, as nearly as possible, the flooding of meadows could be regulated at the time most useful for the maintenance of sedges. This is one option that may be appropriate in future management decisions. A simpler and cheaper method may be to use thermopyles (Fuller, pers. comm.). Possibly, the simplest solution with long-term benefits may well be the implementation of "spray ice" technology. From a biological point of view, the means that engineers resort to, in order to solve the problem may be of little consequence. Of utmost importance, however, is that water is supplied to the Delta at a time and in sufficient volume to restore the life of the Delta to what it was in the pre-Benett Dam days.

The Delta ecosystem has unique characteristics that are of great aesthetic, cultural, and scientific importance. Despite the obvious values of elements of the current, essentially unmanipulated ecosystem in the Park, the impaired status of the Delta will require closer attention in the future. The decline in bison numbers should be a warning of some serious problems in the system and bovine diseases, unless proven otherwise, appears not to be the cause. To quote W. A. Fuller: "...the future of the bison, and many other critters, depends on the reversing of plant succession in the Delta ecosystem. This is overwhelmingly the most important problem facing the Park."

It has been suggested that ranching of other northern populations of bison offers the prospect of increased meat production through improvements in bison husbandry. While the ranching of bison has merits in its own right in non-park areas, any manipulation of bison or predators in the Park would be counter to current National Parks Policy. Should increased manipulation of these resources occur by man outside the Park, then scientific values of unimpaired predator/prey systems, protected from manipulation, will become increasingly more important. Calef (1984) may have hinted of things to come (with respect to bison ranching) with the statement that "hidden in all these proposals are the seeds of destruction of the wilderness — predator control, road building, land clearing, fencing, and competition for good grazing land". On the other hand, the potential for the spread of disease from the Park's bison to domesticated cattle and bison outside the Park, and to the disease-free bison in the Wood Bison Recovery Program (Mackenzie Bison Sanctuary, Hay/Zama Lakes, and Nahanni National Park), must remain a major concern. Future park managers and biologists may be forced to re-evaluate an important cornerstone in park management; namely non-interference.

Many believe that the presence of the "hybrid bison" in Wood Buffalo National Park is undesirable, for two major reasons. First, there is concern that as the wood bison in the Wood Bison Recovery Program multiply and expand their range, they will come into contact and interbreed with the bison in and around the Park, thereby re-introducing plains bison genes into the wood bison gene pool. Second, bison in the Mackenzie Bison Sanctuary are currently considered as disease-free. Contact with Park bison could result in infection of the Mackenzie herd with one or more diseases. We do not want to give the impression that the seriousness of the threat of disease transmission to cattle or to the bison in the Wood Bison Recovery

Program is being minimized; nevertheless, those of us who have worked in the Park feel it is necessary to go on record and to document the value of what currently exists. We believe that evidence is available which suggests that bison currently inside the Park may have much stronger phenotypic affinities to wood bison than would be expected, considering the introduction of more than 6,000 plains bison into the system of about 1,000 animals. Phenotypic criteria ultimately are probably of less value in documenting real differences between wood and plains bison than are genotypic differences (Avise 1989, Geist 1991). The degree of wood bison versus plains bison introgression probably should be evaluated on the basis of molecular genetics before degrees of genetic mixing can be quantified. Studies on the descriptions of phenotypic differences between northern bison in the Mackenzie Bison Sanctuary, those of Wood Buffalo National Park and other areas are currently in progress and should provide interesting insights into conservation of northern bison. We would, however, also emphatically state that the future well being of the Mackenzie herds should be safeguarded, because their presence is of great significance in the conservation of the species.

Maintenance of functional ecosystems and the preservation of species diversity are accepted as fundamental objectives of Park resource management. In the "real" world, the scientific questions are often peripheral to economic and political considerations (Beissinger 1990). With respect to the ecosystem of Wood Buffalo National Park, major decisions about the future of bison and the flooding regime of the Peace-Athabasca Delta must still be made. One can only hope that whatever is ultimately decided, Park resources will be managed in the true spirit of ecosystem conservation, in which the whole is more than simply the sum of its parts.

IX Acknowledgements

Many hours were spent in aircraft by wardens and other field workers; without their contribution the numerical status of bison could not have been documented in this monograph. D. Meleshko, D. McKinnon, and H. Trefry were involved in data collation and computer formatting. This manuscript, or portions thereof at various stages, was reviewed by E. Broughton, C. Carbyn, R. Edwards, C. Gates, W. Fuller, S. Herrero, D. Jaques, R. Leonard, R. McFetridge, M. Meagher, P. McCormack, M. Peterson, W. Stevens, H. Reynolds, S. Tessaro, E. Street, and G. Townsend. We gratefully acknowledge comments provided by those individuals, many of whom have had a long-standing association with bison and with the Park. Much of the material contained in this book was extracted from a 1985 report by S. Oosenbrug and L. Carbyn entitled "Wolf predation on bison in Wood Buffalo National Park." D. Anions participated in all phases of that project and provided a review of the history of bison in the Park. E. Street was instrumental in completing the earlier in-service report entitled "An analysis of the decline of bison in Wood Buffalo National Park from 1971 to 1981, and a status review to 1989." D. Huisman was another co-author of that report and his input to the monitoring of bison numbers in the mid 1980s was an important contribution. P. Debnam and A. Raszewski provided much of the illustrative material.

Much of the earlier work on radio-tracking of collared wolves was carried out with the able assistance of D. West. We thank the pilots M. Bailey, W. Bourque, A. Engst, J. Henniger and I. Ross. P. Jalkotzy collected wolf scat along trails and S. Herrero provided funds and moral support.

C. Gates was very helpful in various aspects of the study, particularly in providing logistical support in May 1990 for field work by the senior author in the Mackenzie Bison Sanctuary and sharing with us his techniques to effectively carry out classified counts. Tim Trottier, Sue and Jeff Turner were wonderful companions in the field. D. Huisman, J. Mercer, M. Peterson, D. Milne and K. Poole (N.W.T. Fish and Wildlife Service) provided unpublished data. S. Barry, D. McKinnon, and M. Kingsley gave valued assistance in the statistical analysis of the data. The research on the journals of fur traders by T. Ferguson provided us with valuable background information into the human/bison relationships in the late 18th and 19th centuries. B. Jones, L. Juba, E. Maloney-Gignac, A. Moore, M. Regnier and

L. Strembitsky typed the manuscript in its various drafts. Most especially we want to thank Cathryn Shanks for paying attention to details in assembling the final draft of the manuscript. D. Dragon, F. Laviolette, residents of Fort Smith, J. Courtoreille, W. Courtoreille, L. Flett, S. Flett, R. Fraser, R. McKay, and A. Simpson, residents of Fort Chipewyan gave many important insights into the historical events involving the management of bison in Wood Buffalo National Park. H. Armbruster, J. James, and M. Regnier provided much needed background support in completing the final draft. We extend our sincere thanks to Bill Fuller, a person of immense experience and wisdom and a man who has been a great inspiration. His careful review of the document was very much appreciated. Any errors or omissions are still our own.

This project was funded by Canadian Parks Service, the Canadian Wildlife Service, the Canadian Circumpolar Institute (CCI) of the University of Alberta, World Wildlife Fund, and L. Carbyn. The interest and support of Superintendents B. Leif, K. East and D. Stewart is gratefully acknowledged. Wardens G. Antoniuk, L. Comin, J. Dixon, D. Milne, M. Peterson, K. Schmidt, and E. Wilson provided friendship and logistical support as did R. Edwards, Canadian Wildlife Service. Special thanks go to C. Hickey and E. Maloney-Gignac (Canadian Circumpolar Institute) and R. Edwards and G. McKeating for encouragement and support provided through the study and to G. McCaughey, who guided the document through its many stages to its completion.

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